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Atso Artimo
Suomen Riistanhoito-Saatio (Finnish Game Foundation)

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Helsinki 1960 . K. F. Puromiehen Kirjapaino O.-Y.

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	18	6	Fig. 6. *For* »*24 = Orivesi*» *read* »*25 = Orivesi*».
	29	6*	*For* »80 %» *read* »72 %».
	30	19	*For* »1—20 km.» *read* »4—20 km.»
			The figures in Tables 1—4 have accidentally escaped correction. The chief errors are:
	43		Table 1, No. 4. *For* »47.2» *read* »43.6».
			Table 1, No. 5. *For* »37.5» *read* »36.0».
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			Table 3. Σ *For* »0.01» *read* »0.1».
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			Table 4, No. 3. *For* »*laqustris*» *read* »*lacustris*».
	56	7*	*For* »4.6» *read* »5.1». *For* »*Typha*, sp.» *read* »*Typha* spp.».
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	68	10	*For* »Crosman» *read* »Crossman.
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	85	11	*For* »1932—54» *read* »1932—58».
	88	1	*For* »longer» *read* »shorter».
	90	16*	*For* »4—120 sq.km./year» *read*» 4—120 km./year».
	93	5	*For* »ALDOUS, S. A.» *read* »ALDOUS, S. E.».
		9*	*For* »BEER, F. R.» *read* »BEER, J. R.».
	94	25*	*For* »CROSMAN» *read* »CROSSMAN».
		12*	*For* »Jour. Wildl. Magt. 20» *read* »Jour. Mammal. 29».
		9*	*For* »M. H. MARKELEY» *read* »M. H. MARKLEY».
	95	10	*For* »Ibid.» *read* »Ecology».
		25*	*For* »GASCHWILER» *read* »GASHWILER».
	96	1	*For* »HAMILTON H. J.» *read* »HAMILTON W. J. Jr.,».
		5	*For* »N. W. MOSLEY» *read* »N. W. HOSLEY».
		8*	*For* »KELLOG, C. E., *read* »KELLOGG, C. E.,».
	98	3	*For* »Liss.» *read* »Nilss.».
		5	*For* »LYNCH, J. I., T. O. O'NEIL» *read* »LYNCH, J. J., T. O'NEIL».
	99	26*	*For* »ROEST, A. J.» *read* »ROEST A. I.».
		14*	*For* »SATHER» *read* »SATHER, J. H.».
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* From bottom.

I. INTRODUCTION

The natural range of the muskrat, *Ondatra zibethicus* (L.), comprises the major part of the North American continent (Fig. 1). In the northern and eastern parts of its range its distribution is more or less continuous, but in the arid west it is very patchy. The species is absent from some areas which, according to Storer (1938), are suitable for it. This writer assumes (op.cit. pp. 159—160) that »Muskrats probably reached some of the now isolated waters of the West during a period when aquatic and palustrine habitats were more widespread, in late Pleistocene or postglacial times. With subsequent contraction of habitat, stocks were reduced and isolated, since when limited subspecific differentiation has occurred. Parallel cases are known among amphibians and fishes in the western states.»

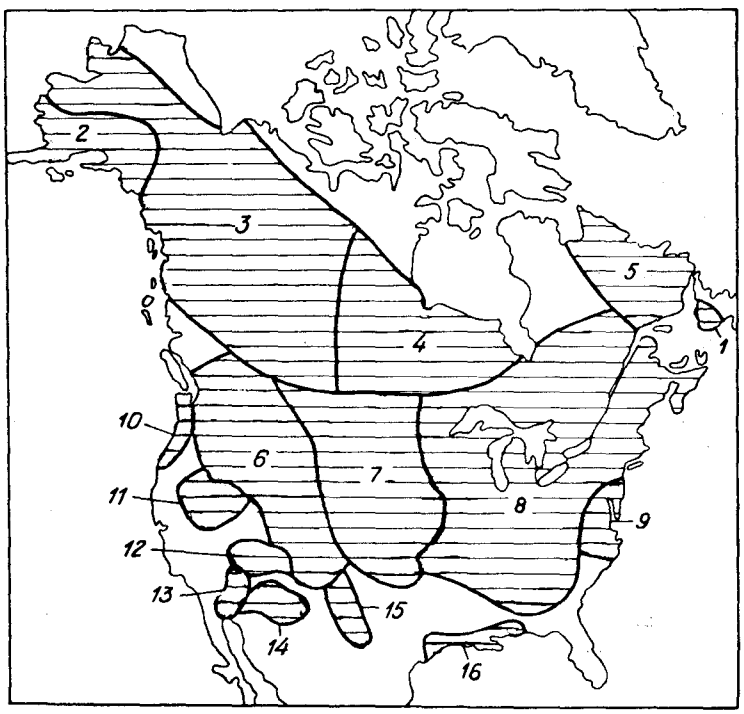

Fig. 1. The natural distribution of Ondatra zibethicus and O. obscurus. 1. Ondatra obscurus, 2. O. z. zalophus, 3. O. z. spatulatus, 4. O. z. albus, 5. O. z. aquilonius, 6. O. z. osoyoosensis, 7. O. z. cinnamominus, 8. O. z. zibethicus, 9. O. z. macrodon, 10. O. z. occipitalis, 11. O. z. mergens, 12. O. z. goldmani, 13. O. z. bernardi, 14. O. z. pallidus, 15. O. z. ripensis, 16. O. z. rivalicius (Hall and Cockrum 1953).

Two species and fifteen races of the muskrat have been described (Fig. 1), but when more investigations are carried out their number will perhaps increase still further.

As a fur-bearer, the muskrat has been trapped since 1638 (Brachrach 1930: 108) and at present it is the most important fur-bearing game animal (Hamilton 1939: 375). Its economic importance has been the reason for attempts to increase its numbers by improvement of conditions and by liberation in new regions or in watercourses from where they had disappeared (e.g. Storer 1938, Sooter 1946, Roest 1951, Durrant 1952). For the same reason, muskrats have been introduced and farmed outside the North American continent. For this purpose, use has been made not only of the nominate race, the common muskrat, *Ondatra z. zibethicus* (L.), but also of the Virginian muskrat, *O. z. macrodon* (Merriam), the fur of which is more valuable. The area of the nominate race comprises Southeastern Canada, the northeastern and east central United States, from New Brunswick and Quebec west to Minnesota, and south to North Georgia and Arkansas, except along the Atlantic seaboard south of Delaware Bay (Hollister 1911). The Virginian muskrat occupies an area comprising the »Middle Atlantic coast region of the United States from Delaware Bay to Pamlico Sound; inland to Washington, Virginia, and Raleigh, N.C.» (op. cit., p. 18).

Enthusiasm for introducing and farming muskrats was very considerable 30—40 years ago among fur farmers both in the animal's native country and in Eurasia (cf. e.g. Storer 1938, Hoffman 1958). In Finland the first importations were made in the 1920's, and in the 1930's farming and liberation were continued with ever increasing rapidity. Muskrats escaped from cages, spread from the areas in which they had been introduced and quickly occupied most of the watercourses in Finland, thus becoming a noteworthy feature of our game (Artimo 1949). When the feral muskrat stocks increased, the farming of muskrats became unprofitable and was abandoned. The number of introductions also decreased and they were restricted to the northern and eastern regions, where spread was slow.

Since the publication of Johnson's (1925) fundamental monograph on the ecology of the muskrat, the animal has become a popular object of investigation both in its native country and in its new areas. The North-American research on muskrats has, thanks above all to Errington, provided valuable additions to our knowledge of mammalian ecology.

In Central Europe, the spread and breeding of the muskrat has been studied in detail, too (e.g. Ulbrich 1930, Hoffmann 1958) and likewise in the British Isles (Warwick 1934, 1940), in France (e.g. Chappelier 1948, Giban et Aubry 1956) and in the Soviet Union, where Lavrov is known for his many investigations and as the author of an extensive survey (1957).

The present author's aim has been to collect data on the introduction of muskrats into Finland and their spread from the places of liberation, to investigate the factors affecting their spread and acclimatization, and hence to try to establish a basis for the rational care of our muskrat waters. The author has studied various aspects of muskrat ecology and compared the results obtained with those of the American investigators. Since the parasites and diseases of Finnish muskrats have so far received no systematic study, these subjects could not be given the attention they deserve. It seems evident, however, that the muskrat stocks introduced into Finland have been very healthy (Lampio 1946) and remained so, for no mass deaths due to diseases have been recorded in Finland. Steady and effective trapping of the muskrat stocks has prevented overpopulation, and the establishment of stocks suffering from lack of food and susceptible to diseases has obviously not occurred here. The situation has been the same in Central Europe (Hoffmann 1958) and in the Soviet Union (Novikov 1936 a, Vasiljev 1939, Lavrov 1953). For this reason no attempt has been made in this study to investigate diseases and parasites.

The actual field studies were carried out in the period 1944—1949, mainly in the Kokemäenjoki drainage basin, which has long been a strong muskrat region, and in Uusimaa in the districts of Riihimäki and Lohja. Shorter field trips have been made to the districts of Rauma, Lappeenranta and Kuopio.

A preliminary report on the care of our muskrat waters was published by the author in 1949, and in some other papers the ecology of muskrats has been dealt with (Artimo 1952, 1953, 1957). In the present paper, attention has mainly been focussed on the process of acclimatization and on the more theoretical aspects of this problem.

Acknowledgements. I am greatly indebted to the Director of the Game Research Institute, Dr. Lauri Siivonen, for having entrusted me with the present theme, incorporated in the research programme of the Institute, and for the encouraging interest he has shown throughout in my work.

My pleasant duty is also to thank Prof. Olavi Kalela and Prof. Ernst Palmén for critically reading the manuscript. My thanks are also due to Dr. Jaakko Jalas, Assistant Professor of Botany, who has checked certain botanical terms and the botanical nomenclature.

Further I wish to thank Mr. Sulo Nuorvala for the translation of my manuscript into English and Mrs. Jean Margaret Perttunen for checking the language. Acknowledgements are also due to Miss Toini Tikkanen, who has drawn the figures.

For this study I have received grants from the State of Finland, the Finnish Academy of Science and from the Societas Zoologica Botanica Fennica 'Vanamo'.

II. HISTORY OF INTRODUCTION INTO FINLAND

A. Material

1. Earlier accounts

There are detailed accounts of some earlier introductions and of the initial distribution of muskrats in Finland (Andbacka 1923, 1924, Ahonen 1924, Korvenkontio 1924, 1925, 1926, Liro 1924, 1925). Klemola (1936, 1937 a) published maps of the localities in which these animals had been introduced by 1935. On the basis of over 400 inquiries sent out by the Association of Finnish Fur Farmers, Lilja (1932) published a distribution map showing the extent of the area occupied by muskrats in this country in 1931. On the basis of the records of the Game Research Institute, the present author (Artimo 1945) reviewed the decline of our muskrat stock in 1944 and later published short summaries of the history of the spread of the species and maps of its range in Finland in 1925, 1931, 1945 and 1948 (Artimo 1949), and in 1927, 1937 and 1954 (Artimo 1956). In addition, maps of the population densities and of the distribution of muskrat populations since the year 1950 were compiled by the Game Research Institute of Finland (Anonymous 1950, Siivonen & Väänänen 1951, Väänänen 1952, 1953, 1954, Selin 1956, 1957, Mörsky 1958).

Local accounts and notes on the introduction and distribution of muskrats have also appeared in various other periodicals (Fiskeritidskrift för Finland, Luonnon Ystävä/Luonnon Tutkija, Metsälehti, Metsästys ja Kalastus, Suomen Kalastuslehti, Tidskrift för Jakt och Fiske, Tidskrift för Jägare och Fiskare, Turkistalous) and in the newspapers.

2. Data from archives

The following data from archives have been utilized:

Among the papers of the late Dr. V. Korvenkontio there is a sketch of the area of distribution of muskrats in 1925. In these records there are also scattered notes and observations, mostly referring to Uusimaa and Häme and press-cuttings giving information about further introductions. This material is now in the keeping of the Game Research Institute of Finland.

In the archives of the Ministry of Agriculture (MA) there is a collection of records of muskrat importations and introductions sent in by different persons to the game inspector, and a map of the Finnish range of the muskrat in 1937 made by the game inspector of that time (V. Klemola).

From the archives of the State Board of Forestry the author obtained a list of all the releases of muskrats carried out by this institution. In the same archives there are also letters sent by private persons announcing introductions and newly occupied localities particularly regarding northern and eastern Finland, from where other reports have been less frequent.

Dr. L. Siivonen placed at the author's disposal his valuable and very detailed records on the introduction of muskrats in Pieksämäki and their spread in this region. These records are based on an inquiry made through the newspapers and supplemented by letters addressed to many private persons, and on Dr. Siivonen's extensive excursions on the region in question in the years 1935 and 1936.

3. Inquiries and other sources of data

In the yearly game reports of the 200 or so members of the Finnish Hunters's Association (FHA) there is also information on new localities of the muskrat and notes on the size of the muskrat stock and of new introductions. These notes appeared in the Association's reports from 1928 until 1948. After this, and to some extent since the year 1945, these were replaced by the corresponding annual reports of the Game Research Institute, which are based on information from approximately 500 observers (cf. Siivonen 1957). From these reports it has been possible to follow the spread of muskrat stocks and the fluctuation in their numbers from commune to commune throughout the country.

In 1945, the Game Research Institute (GRI) carried out through its observer network a general survey of the introductions undertaken and the spread from these. Other observations elucidating different aspects of the ecology of muskrats were also requested. A total of 491 answers (from 391 communes of Finland) were received. The replies to the annual inquiries of the Game Research Institute on the amount of game stock also contain information on the size and spread of muskrat stocks, of their fluctuations in numbers, and other observations on the ecology of muskrats. In addition, the Game Research Institute has addressed inquiries to numerous private persons. In 1946, the Game Research Institute sent to all professional fishermen and persons whose part-time occupation is fishing, to fishery advisers and to piscicultural stations an inquiry asking for information concerning damage caused by muskrats. Altogether 423 answers were recived.

During his excursions the present author has made a number of additional inquiries. In this way, confirmation and more precise details regarding incomplete records were obtained. Further, it was possible to obtain information about some introductions on which no documentary evidence was available.

B. Introductions

1. The origin of the animals introduced

According to the archives mentioned above, altogether 103 specimens of muskrats were imported from Czechoslovakia. These muskrats were obviously descendants of a population belonging to the nominate race (Müller 1952, 1953) imported into Czechoslovakia from Ohio.

In addition, it is estimated that about 700 specimens belonging to the nominate race were imported from Ontario, Canada.

The number of animals of the black phase of the Virginian muskrat, *O. z. macrodon* (Merr.), also known as the blue muskrat, imported from Maryland and Pennsylvania (cf. Koski 1946), U.S.A., is unknown. According to the information available, about 300 blue muskrats may have been introduced into different parts of Finland, but some of these may have been reared on Finnish fur farms.

It can thus be established that a total of at least 800 specimens of the nominate race and hardly more than 300 Virginian muskrats have been imported into Finland. The majority of the liberations carried out in Finland involved specimens reared on native fur farms, or feral specimens caught and transferred elsewhere.

2. Types of introduction and numbers of animals involved

The introductions carried out can be grouped as follows:

a. Introductions by private persons or concerns were made in water systems owned or rented for this purpose in order to obtain furs in amounts calculated from American examples (e.g. Andtbacka 1923, 1924, Korvenkontio 1925, Koskelo 1931, Lilja 1932). Although the muskrats throve and bred well in water systems suitable to them, the catches remained very small and the economic calculations proved overoptimistic. The animals, however, quickly spread to the surrounding waters.

b. Fur farming under so-called semi-wild conditions, i.e. in lakes or bays of lakes fenced with wire mesh screen in order to keep the muskrat population within a restricted area. Some such farms were established in the 1930's, but the initial outlay proved to be too high in comparison with the profits, and the animals evidently escaped from them without difficulty.

c. Muskrat farms where the animals were kept in cages. In the beginning, this seemed to be very profitable, because there was a great demand for muskrats

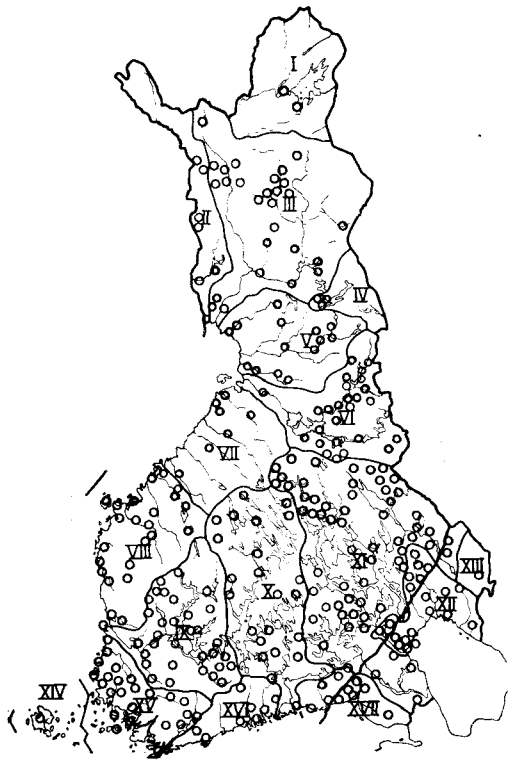

Fig. 2. Introductions of muskrats carried out in different water-system areas. (I = Area of the Arctic Ocean, II = Tornion-Muonionjoki river basin, III = Kemijoki drainage basin, IV = Area of Kuusamo, V = Simo—Kiiminkijoki water-system, VI = Oulujoki drainage basin, VII = River basins of the northern parts of Pohjanmaa, VIII = River basins of the southern parts of Pohjanmaa, IX = Kokemäenjoki drainage basin, X = Kymijoki drainage basin, XI = Vuoksi drainage basin, XII = Ladoga area, XIII = Suojoki river basin, XIV = Ahvenanmaa Islands, XV = River basins of S. W. Finland, XVI = River basins of Uusimaa, XVII = River basins of the eastern parts of the Gulf of Finland.)

for introductions and for furs. In the 1930's there were many such muskrat farms from which specimens regularly escaped. As the natural muskrat populations originating from liberated and escaped specimens increased, such farms became unprofitable and were therefore gradually abandoned.

d. Liberation was the last method to come into vogue. The animals were released in water systems rich in vegetation with the object of creating muskrat stocks of economic value. The liberations made by communes, by the Ministry of Agriculture, timber firms, fur firms, hunting and fishing societies and above all by the State Board of Forestry and some introductions carried out by private persons fall into this group.

The first liberation in Finland was carried out in 1919—1920 in Lake Ruuhijärvi near the town of Kajaani (in area VI, Fig. 2, information by letter from V. Haapalainen on 28. Nov. 1954). This attempt was evidently not very successful, because later specimens were reintroduced into the same localities. This

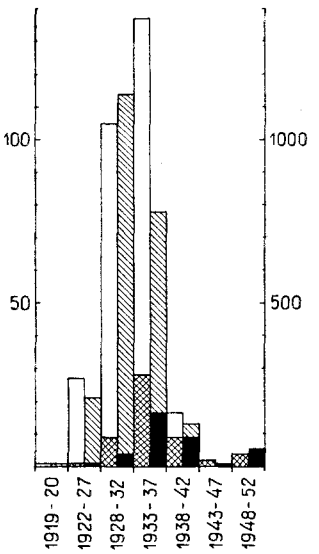

Fig. 3. Numbers of muskrat introductions during different years. (White = number of introductions, scale at left; hatched = number of specimens released, scale at right. These columns represent the situation in the entire country, the cross-hatched and black columns the corresponding numbers in North Finland.)

liberation, at least, seems not to have had any significant effect on the establishment of the muskrat stock or its spread as regards either the whole country or even the waters in question (Artimo 1956). The second liberation which is referred to in the earlier literature as the first (Korvenkontio 1925, Liro 1925, Artimo 1949 etc.) was made in 1922 in Kruunupyy (in area VIII, Fig. 2). It was from this liberation that the wild muskrat stock in Finland began to increase and spread.

In the 1920's and 1930's much propaganda was made for the release of muskrats (e.g. Korvenkontio 1923, 1925, 1926, 1929 a, b, Andtbacka 1924, Koskelo 1931, 1932, Lilja 1932 etc.). On the other hand, many writers obviously feared that the muskrat might become as great a pest here as in Central Europe (e.g. Suomalainen 1923, Brander 1924, Liro 1924, 1925). In spite of this, animals were liberated in at least 293 localities from Hankoniemi to Inari (Fig. 2).

The interest in introductions varied remarkably in different periods (Fig. 3). It reached its peak in the years 1933—37, when altogether 137 liberations were made, whereas the number of specimens released was highest in the years 1928—32 (1144 specimens). The wild muskrat stock gradually increased, and after 1937 introductions were made only in remote districts in Central and North Finland.

The majority of the introductions (61) were made in the Vuoksi drainage basin (Fig. 4). Only one introduction was made in the Ahvenanmaa Islands and in the Suojoki river basin.

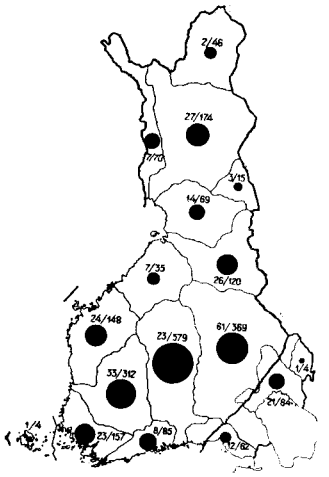

Fig. 4. The numbers of muskrat released in different water-system areas. (The numbers indicate the number of introductions and the number of specimens released.)

In 28 % of cases it has not been possible to ascertain the number of muskrats released. The highest number of pairs (200) was liberated in Lake Kirkkosurnunen in Pieksämäki (in the area X, Fig. 2). The next in order were: 50 pairs in Lake Kuusjärvi (Virrat, in the area IX), 58 specimens at Häggesböle (Kirkkonummi, XVI) and 20 pairs in Lakes Kirakkajärvi (Inari, I), Portimojärvi (Ylitornio, II) and Kiurujärvi (Savonranta, XI). All other liberations consisted of less than 20 pairs. Releases of one pair only were made in 15 localities. In one case (Lake Keskijärvi in Pudasjärvi, V) one member of the pair to be introduced died on the way. Soon after the release of one pair in Lake Puurijärvi in Kauvatsa (IX) one of the specimens was found dead. Most of the liberations consisted of 2 pairs. To get an approximate idea of the number of muskrats introduced, two pairs have been assumed to have been released in the cases where it has not been possible to find out the actual number of specimens. Calculated in this way, the total number of muskrats introduced would amount to about 2300 specimens. The greatest numbers of specimens (579) were released in the Kymijoki drainage basin (Fig. 4).

It seems very probable that in most cases populations became established, increased and spread to adjacent water systems. Only 50 introductions are known with certainty to have failed.

The blue muskrat, which was liberated in perhaps 46 localities, proved less successful than the nominate race. Blue muskrats, however, may still be living in some of their sites of release, because, in the opinion of fur farmers, 2—3 % of the total muskrat catch consists of blue muskrats. Most of these are found in the

Saimaa area, where they constitute about 10 % of the annual catch. Unless otherwise mentioned, the following account deals with the nominate race, but for purposes of comparison the fate of the blue muskrat is very significant.

C. Dispersal from several centres of introduction

It has not been considered necessary to describe in detail the dispersal of muskrats from every known place of liberation. Analyses of them are kept in the archives of the Game Research Institute. The following survey presents only some typical examples. The examples are from those watercourses for which the most detailed information is available on the development of the muskrat stock since its introduction.

1. Dispersal in the river basins in the northern parts of Pohjanmaa

In 1923, 5 pairs of muskrats were introduced in the middle course of the Kalajoki river basin in Ylivieska Commune (Ahonen 1924, Korvenkontio 1925, Liro 1925). In 1924 and in 1925, emigrations took place from this centre (Fig. 5). Through bogs and ditches they spread, especially during flood-time, to Sievi (in 1924) and from there on over the watershed to Kannus Commune (1925) in the Lestijoki river basin. In the Kalajoki river basin they spread to Lake Reisjärvi in the upper course and from there continued over the watershed to Lestijärvi Commune. They reached the upper course of the Lestijoki river basin in 1925. Muskrats also spread along the Kalajoki river basin to Nivala (1924) and Haapajärvi Communes in its upper course. Individual specimens obviously crossed a local watershed and in 1925 reached the upper course of the Pyhäjoki river basin. From here they continued further over the main watershed to the Vuoksi drainage basin, where in the same year (1925) they reached Kiuruvesi Commune (Juvelius 1926). Alavieska, in the lower course of the Kalajoki river basin, was reached in 1924—25. The animals were also observed in Merijärvi Commune in the lower course of the Pyhäjoki river basin. Further outposts were established in the area of this river basin in Haapavesi and Kärsämäki Communes, from where the muskrats extended their emigrations up to the Siikajoki river basin (in Piippola and in Pulkkila Communes). In the north they reached Vihanti and Liminka Communes in 1924. During this expansion (1923—25) localities to a distance of 60 km. and up to 120 km. from the site of release were reached. The watersheds between the river basins apparently did not hinder or even delay the

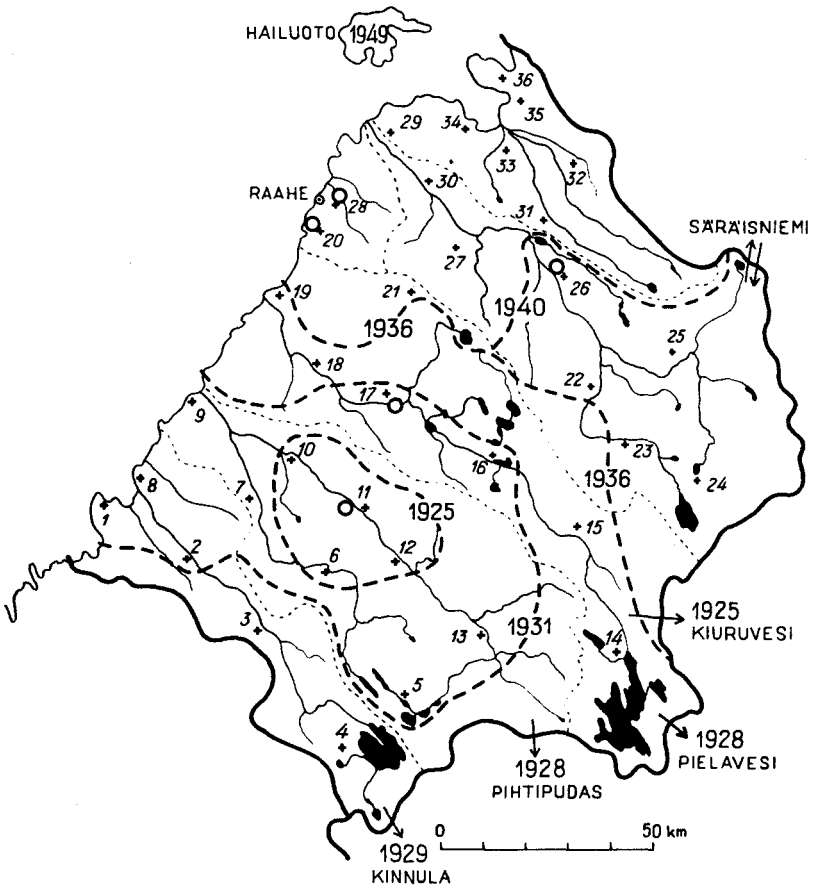

Fig. 5. The dispersal of muskrats from the centre of release in Ylivieska to the river basins of the northernmost parts of Pohjanmaa (area VII, cf. Fig. 2) in the years 1923—49 (O = sites of release; 1 = Lohtaja, 2 = Kannus, 3 = Toholampi, 4 = Lestijärvi, 5 = Reisjärvi, 6 = Sievi, 7 = Rautio, 8 = Himanka, 9 = Kalajoki, 10 = Alavieska, 11 = Ylivieska, 12 = Nivala, 13 = Haapajärvi, 14 = Pyhäjärvi, 15 = Kärsämäki, 16 = Haapavesi, 17 = Oulainen, 18 = Merijärvi, 19 = Pyhäjoki, 20 = Saloinen, 21 = Vihanti, 22 = Pulkkila, 23 = Piippola, 24 = Pyhäntä, 25 = Kestilä, 26 = Rantsila, 27 = Paavola, 28 = Pattijoki, 29 = Siikajoki, 30 = Revonlahti, 31 = Temmes, 32 = Tyrnävä, 33 = Lumijoki, 35 = Kempele, 36 = Oulunsalo).

emigrations! At the periphery of their distributional area, the muskrats probably could not become permanently established, but perished before long; only reports of their absence were received in the following years (FHA). In the original site of liberation and for about 20—30 km. around it (cf. Ahonen 1928), however, the population increased. This is shown by a newspaper report (Uusi Suomi 14. 10. 1927) according to which muskrats were very abundant in the middle reaches

of the Kalajoki river basin and in adjoining waters and by the fact that in Ylivieska (1929) about 600 muskrats were caught (FHA). They were also found in isolated lakes and woodland pools.

A further clearly observable peripheral expansion took place in the years 1926—31, after which the muskrat stock in the main area decreased remarkably (FHA, Lilja 1932). During this expansion muskrats spread to Rautio and Kalajoki Communes in the mouth of the river basin in which the first introduction had been made. They further settled in the mouth of the Lestijoki river basin (Kannus, Lohtaja, and Himanka Communes) in 1926—28. A permanent population also developed in the upper course of the Kalajoki river basin (in Haapajärvi 1926 and in Reisjärvi in 1930). From there the expansion extended further over the watershed to Pihtipudas Commune in the drainage basin of the Kymijoki (1928) and to Pielavesi Commune in the Vuoksi drainage basin (1928). In the north it reached the middle course of the Pyhäjoki river where a strong population has developed in Oulainen and Haapajärvi Communes (since the year 1931). The introduction made in 1930 in Oulainen obviously had no effect on the settling of muskrats in this area, because at the same time numerous muskrats emigrated there from Ylivieska. From here pioneers wandered to Vihanti, Paavola, and Revonlahti Communes (1931) in the Siikajoki river basin, but no colony became established there. During the expansion, permanent populations were found up to 40—50 km. from the centre in Ylivieska, and pioneers were observed at distances of up to 80—90 km. (Pielavesi, Pihtipudas, Paavola, Revonlahti).

In the mouth of the Lestijoki river and in the middle course of the Pyhäjoki river the populations increased remarkably, and a new period of expansion followed during the years 1932—36. By 1935, the shores of the Lestijoki river were tenanted by muskrats probably originating from the lower course of the river. As muskrats were found in Toholampi Commune at the same time (1932—33) as in Lestijärvi, the upper course of the Lestijoki water system was perhaps occupied by muskrats from the Kalajoki river basin (Reisjärvi) from which some pioneers had reached Lestijärvi even earlier (1925, cf. above). From Lestijärvi the expansion extended to the upper course of the Kymijoki drainage basin as far north as Kinnula (1933). The entire Kalajoki river basin was colonized, and from the middle course of Pyhäjoki this river was entirely occupied by 1936. The muskrats continued their emigration from Haapavesi over the watershed to the lower course of the Siikajoki river basin (Paavola), but did not become established. As a result of a third expansion, the muskrats occupied areas about 60 km. from Ylivieska, but pioneers were observed at a distance of as much as 80 km.

In the years 1937—40 a strong expansion was observed from Haapavesi to the upper course of the Siikajoki and from here to its middle course. Muskrats

were seen in Piippola, Pulkkila, Kestilä (1937) and Pyhäntä (1938) Communes, and their movements were observed in 1939—40 in the drainage canals of the Pelso bog. Movements of muskrats were also noted from the river basin of the Oulujoki (Säräisniemi) to the upper course of the Siikajoki river basin and *vice versa*. In Rantsila Commune the muskrats became settled in 1938—39. Animals were also released here at about the same time, but no detailed information concerning the results are available. During this expansion the muskrat became permanently settled in a region up to 80—100 km. from Ylivieska, whilst pioneers from Rantsila or from Oulainen were found in Paavola, Liminka and further in Lumijoki and Tyrvänä (1938) and Temmes Communes (1940). The permanent population in the upper course of the Temmesjoki probably spread from Rantsila. Not until the 1944—49 expansion did muskrats occupy all the regions in the mouth of the Siikajoki river and the river basins of Temmesjoki and Liminka. Possibly this invasion partly took place from the muskrat farm at the mouth of the Siikajoki (in 1933—35). In Pattijoki and Saloinen Communes muskrats were also released in the isolated lakes Haapajärvi and Viitajärvi (in about 1933—35) but it is not possible to estimate the result, because muskrats reached these areas simultaneously from elsewhere.

On the island of Hailuoto (Syökari) the first muskrats were found in 1949 (some winter houses; H. I. Isola, GRI). Presumably they had been released there, although no information about this can be obtained.

2. Dispersal in the southern parts of the Kokemäenjoki drainage basin

In 1923, altogether 29 specimens of muskrats were released in the southern parts of the Kokemäenjoki drainage basin (Fig. 6) in Tuulos and Hauho Communes (Korvenkontio 1925, Liro 1925, Häppölä 1928). From these populations a distinct expansion took place. In 1924, muskrats were already found in Vanaja and Riihimäki and in the city of Tampere (Anonymous 1925 a, b, Korvenkontio 1926) at a distance of 65—75 km. from the site of release, but no permanent colony developed here. By 1925, only the waters near the sites of release were occupied permanently at a distance of about 20 km. (Lakes Roine, Hauhonselkä, Ilmoilanselkä, the southern parts of Lake Kukkia and the shores of Pyhäjärvi). In these lakes the muskrat populations increased with enormous rapidity (Letter of Hj. Schulman Dec. 22, 1925, A. Pakkala, GRI; Anonymous 1925 a, Muhojärvi 1927).

During a strong expansion in the years 1926—30 the muskrats spread to a distance of 40—45 km. from the main area. In the Vanaja watercourse they reached Hausjärvi (in 1928—29, Anonymous 1930 a) and Kärkölä (1930) Communes

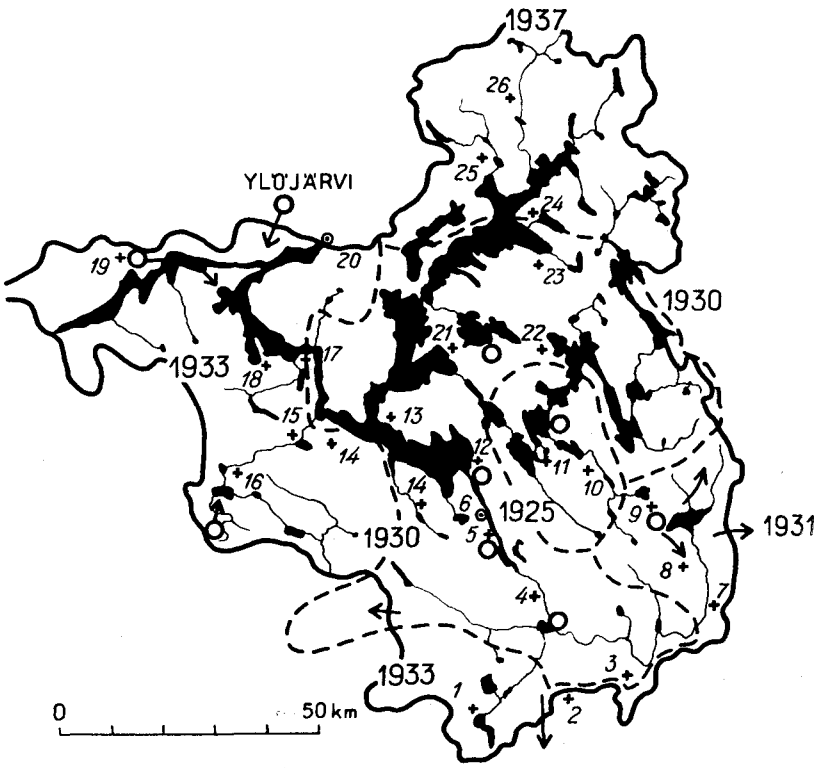

Fig. 6. The dispersal of muskrats in the southern parts of the Kokemäenjoki basin in the period 1923—37 (area IX; 0 = sites of release; 1 = Loppi, 2 = Riihimäki, 3 = Hausjärvi, 4 = Janakkala, 5 = Vanaja, 6 = Hämeenlinna, 7 = Kärkölä, 8 = Koski, 9 = Lammi, 10 = Tuulos, 11 = Hauho, 12 = Tyrväntö, 13 = Sääksmäki, 14 = Kalvola, 15 = Kylmäkoski, 16 = Urjala, 17 = Lempäälä, 18 = Vesilahti, 19 = Karkku, 20 = Tampere, 21 = Pälkäne, 22 = Luopioinen, 23 = Kuhmalahti, 24 = Eräjärvi, 24 = Orivesi, 26 = Juupajoki).

up the Puujoki river. Here the muskrats emigrating towards the upper course merged with a population spreading from the 1930 introduction in Lake Pääjärvi, from where the expansion also extended over the watershed to Hollola Commune (1931, MA) in the Kymijoki drainage basin. Liberations made near the town of Hämeenlinna and in Janakkala Commune in some isolated woodland pond (1928—29, Hakola 1931) seem not to have had any noteworthy effect on the distribution of the muskrats, which spread simultaneously to these regions from the direction of Hauho and Tuulos. The animals then emigrated through Janakkala to Renko Commune (1928) and from here over the watershed to the Loimijoki river basin and to Loppi and Riihimäki in the Vantaa river basin (1930). At the same time when the muskrats reached there from the centres in Hauho and Tuulos, some

animals were released at the mouth of the Vanaja watercourse in Tyrväntö Commune (1925).

Along the shores of Lake Vanajavesi the muskrats spread up to Kalvola (in 1926—27) and in the years 1928—29 to Lempäälä (Anonymous 1929). In the north they reached Lake Jouttesselkä in Luopioinen (1926) and Längelmävesi in Kangasala, Sahalahti and Eräjärvi Communes. In 1926, a few individuals were found in Orivesi Commune. Towards the north-east the expansion continued across Luopioinen in 1926—27 (Korvenkontio 1926, Saravuori 1933) and beyond to Kuhmalahti (1928), and Lammi (1926, Lake Kuohijärvi) and up to the borders of Padasjoki Commune in 1928 (Böök 1928). New colonies developed in the occupied regions in Janakkala, Kalvola, and in the southern parts of Lake Längelmävesi. In Kalvola, for instance, about 1200 muskrats from Lake Kalvolanjärvi were shot during two weeks in 1929 (E. Huti, GRI). This high number of muskrats indicates that invasions had taken place from elsewhere. In the watercourse of Längelmävesi the muskrats were so abundant that they even nested under stones on barren islands (Korvenkontio, GRI). Such nesting has not been noted since then in this region and the author does not know of any such cases elsewhere. From the same period (1929) there are reports from Janakkala of great damage inflicted by muskrats burrowing in the embankments (MA). From these centres a strong expansion began in the years 1930—33. From Kalvola this extended to Kylmäkoski in the Viialanjoki watercourse in 1931 (Lilja 1932, Saravuori 1933) where muskrats also spread later from the population introduced in Urjala Commune (1933) and further to Lempäälä Commune in 1930—31 and to Vesilahti. Here, in 1933, the animals merged with the muskrats spreading from Ylöjärvi (1926) or Karkku (1930) Communes. From the centre at Längelmävesi a strong expansion took place up the watercourse. Juupajoki Commune was reached in 1933, and by 1937 the whole Längelmävesi watercourse had obviously been colonized. In the south, the muskrats from Janakkala Commune reached the southern parts of Loppi in 1932—33. Thus everywhere the muskrats had reached the watersheds at the periphery of the drainage basin and locally had dispersed over these into other drainage basins. From the centres of introduction in Hauho and Tuulos Commune they had thus spread over a radius of 60—80 km.

3. Dispersal in the northern parts of the Kokemäenjoki drainage basin

In 1929, fifty pairs of muskrats were released in the commune of Virrat (Fig. 7). The expansion of this population started during the next two years; adjacent waters at a distance of about 20 km. were occupied within this time. Some individuals were found in Vilppula (50 km. distant) but no permanent population was

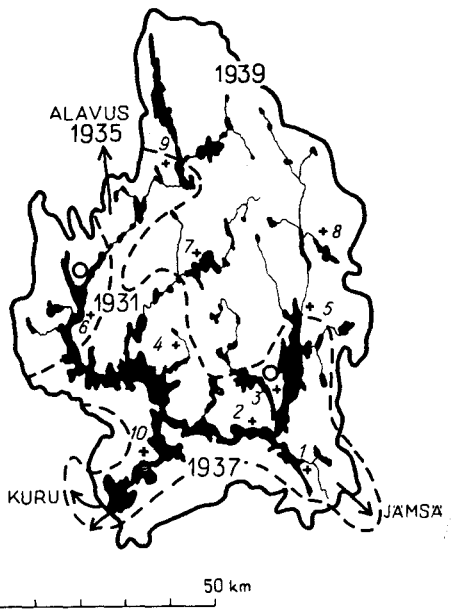

Fig. 7. The dispersal of muskrats in the northern parts of the Kokemäenjoki basin in the period 1929—39 (area IX; 0 = sites of release; 1 = Kuorevesi, 2 = Vilppula, 3 = Mänttä, 4 = Pohjaslahti, 5 = Keuru, 6 = Virrat, 7 = Pihlajavesi, 8 = Multia, 9 = Ähtäri, 10 = Ruovesi).

formed there. A remarkable increase was observed in the main area in 1934—37. During this period a new expansion took place. In the north the muskrats reached Ähtäri in 1934 and by the year 1937 the middle parts of this commune had been invaded. In 1939, the northernmost parts of this watercourse were occupied. Emigration over the watershed (1934—35) to Alavus Commune, i.e. to the river basin in the southern part of Pohjanmaa (area VIII, Fig. 2) was also observed, and another expansion to Pohjaslahti and southwards to Ruovesi (1934) Commune. In the following year the animals were already noted in Kuru Commune, to which they had simultaneously spread from the Ylöjärvi centre in the south. In 1935 muskrats were found in one lake of the Pihlajavesi watercourse (MA). The middle reaches of the watercourse were occupied by 1937 and the whole watercourse by 1939. The southern parts of the Keuruu watercourse in the east were invaded in 1936—37. In Vilppula Commune the first pioneers, which were observed as early as 1931, disappeared without leaving any trace, but in the years 1934—37 muskrats were observed there in ever increasing numbers. Emigration from the direction of Virrat was very frequent. From here the pioneers reached Multia Commune and, in 1936—37, the northern parts of Keurusselkä Lake became permanently settled. Kuorevesi was occupied in 1935 and from there the muskrats spread over the watershed to the Jämsänjoki watercourse in the Kymijoki drainage basin (1935, area X, Fig. 2). The years 1936—37 were everywhere

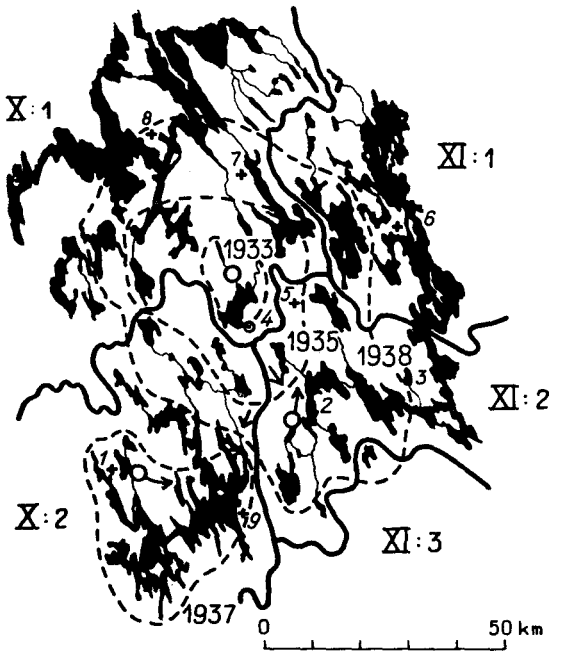

Fig. 8. The dispersal of muskrats from the introduction in the watershed area of Pieksämäki in the period 1932—40. (Mainly according to Dr. L. Siivonen, GRI. Area X: 1 Rautalampi watercourse, : X2 Mäntyharju watercourse, XI: 1 the area of Iso Kalla, XI: 2 the area of Haukivesi, XI: 3 the area of Saimaa-Puruvesi; 0 = sites of release; 1 = Kangasniemi, 2 = Virtasalmi, 3 = Joroinen, 4 = Pieksämäki, 5 = Jäppilä, 6 = Leppävirta, 7 = Suonenjoki, 8 = Rautalampi, 9 = Haukivuori.)

years of increase, and the southern parts of the watercourses of Kuorevesi—Keuruu were invaded. In the years 1937—39 an expansion again took place and the upper course of the water basin was occupied. It is true that 2 pairs were released at Kolho near Vilppula (1934), but by this time muskrats from Virrat had already reached the area and hence the quick and extensive occupation of parts of this watercourse cannot be attributed to this liberation, but rather to an unusually strong expansion from the direction of Virrat.

4. Dispersal from the introduction in the Pieksämäki watershed region

The greatest liberation of muskrats conducted in Finland (200 pairs) was made in Pieksämäki Commune (Fig. 8) in 1932. These muskrats were originally intended for the Soviet Union, but because of the early winter the plans were changed and the animals were released in October in Lake Kirkkosurnunen in Pieksämäki. Soon after this the waters froze. The number of animals released was much too large for this small lake, and the fencing, which reached some way around both the sides of the outlet, proved to be no barrier. In the winter of 1932/33 there were 10 winter houses in the lake, indicating that the majority of the

muskrats had moved away at once. By the autumn of the year 1932, muskrats were found in Pieksänjärvi Lake (into which Lake Kirkkosurnunen empties its waters). In the winter of 1936/37, only 3—4 winter houses were found at the site of release.

In 1933, the animals were observed only in the lake where they had been released and in some adjacent lakes and pools. The first pioneers were found at a distance of 24 km. northwest of Lake Pieksänjärvi. In this year conditions for reproduction were favourable and a great expansion took place in 1933—35. Then the muskrats occupied water systems situated about 20—30 km. from the site of release. Through the outlet from Pieksänjärvi they spread about 30 km. northwards into the watercourse of Rautalampi (Fig. 8, watercourse area X: 1) and into the southern parts of Lake Suonteenselkä. In the east they spread to the commune of Jäppilä into the watercourse of Haukivesi (area XI: 2) 30 km. from the site of release. In the east and southeast Lake Längelmävesi in Virtasalmi Commune was reached. The muskrats may also have spread here from the introduction made in 1933 in Virtasalmi (6 pairs). In the south the distributional area reached to the northernmost parts of the watercourse of Mäntyharju (X: 2, Lake Iso-Naakkima) and from here to the watercourse of Rautalampi (X: 1). Pioneers were observed in Suonenjoki and in Tervo sound (about 40 km. from the site of release) and in the Haukivesi region they were also found near Joroinen (40 km. from the site of release).

A new expansion took place in 1936—38. Towards the north-west muskrats spread to Iisvesi and Koskelonvesi Lakes and to the neighbourhood of the village of Rautalampi in the watercourse of Rautalampi (X: 1). In the north-east the first muskrats were found in Leppävirta Commune in the region of Iso-Kalla (XI: 1) and occupied the shores of Lake Sorsavesi. The expansion extended to Joroinen, towards the east and southeast, further to the region of Haukivesi (XI: 2), and partly even to the region of Saimaa—Puruvesi (XI: 3). In the south in the commune of Haukivuori Lake Kangasjärvi was occupied. In the south-east (X: 2) these animals met the population spreading to Lake Kyyvesi from the introduction made in Kangasniemi in 1938. Animals were also released in about 1931 in some woodland pool in the commune of Haukivuori but no information regarding their further history is available. When, eventually, muskrats occupied some water areas in the east in 1939—40, they had everywhere reached great lakes where they met other expanding populations.

5. Dispersal in the coastal area of Uusimaa

In 1924, 58 muskrats were introduced at Heggesböle, in Kirkkonummi Commune (Korvenkontio 1925, Liro 1925). Rapid expansion along the bay of Espoo

took place in the years 1924—29 (Fig. 9). A large colony of muskrats was found there in 1928, in the west the base of the Porkkala peninsula was reached. The first pioneers were observed at Evitskog in the north (distance 20 km., in 1928) and near Helsinki in the east (30 km. from the site of release, in 1928, Korvenkontio, GRI, Anonymous 1928 a) and in Inkoo Commune in the west (about 30—40 km. from the site of release).

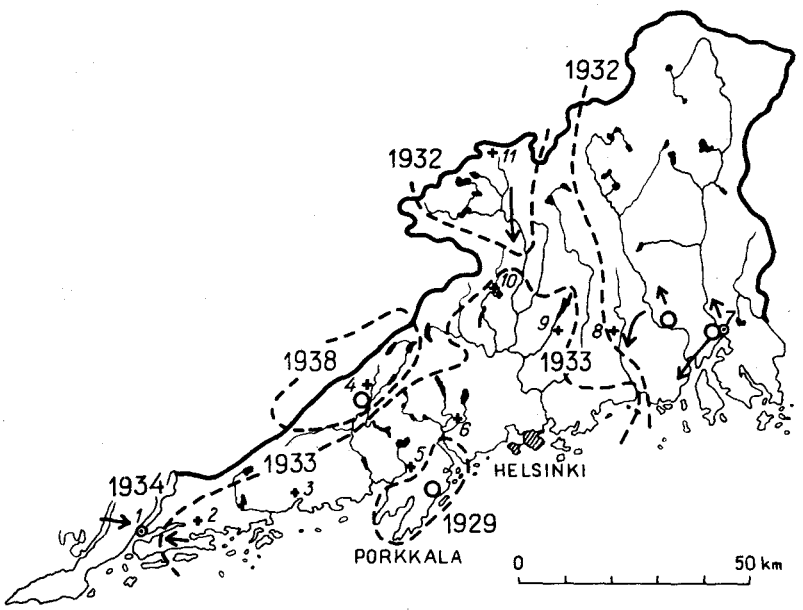

Fig. 9. The dispersal of muskrats in the western parts of the coastal area of Uusimaa in the period 1924—38 (area XVI; 0 = sites of release; 1 = Tammisaari, 2 = Snappertuna, 3 = Inkoo, 4 = Siuntio, 5 = Kirkkonummi, 6 = Espoo, 7 = Porvoo, 8 = Sipoo, 9 = Tuusula, 10 = Nurmijärvi, 11 = Riihimäki).

In the years 1928—33 the muskrat population of Kirkkonummi was very abundant (Anonymous 1928 b, Korvenkontio, GRI; FHA; Lilja 1932). From the main area with a radius of only 10 km. a second expansion followed in 1930—33 into the northern parts of Espoo and Kirkkonummi Communes (in 1931) and even to some outer islands of the Gulf of Finland, where they were observed on the island of Makilo in 1930 (Anonymous 1930 b). In the east, muskrats were found in Sipoo Commune, east of Helsinki, where in 1933 they met muskrats spreading from the direction of the city of Porvoo. The area of distribution extended northwards along the river Vantaa to Tuusula (1931) and to Nurmijärvi (1932) Communes. In 1933, the animals were met there by the population spreading from

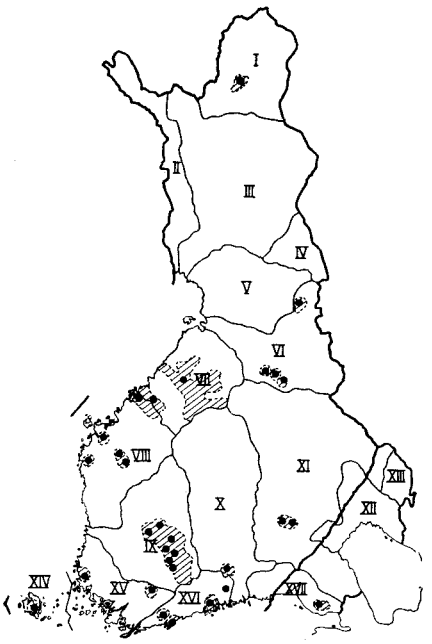

Fig. 10. Muskrat introductions and the extent of their distributional area up to the end of 1927.

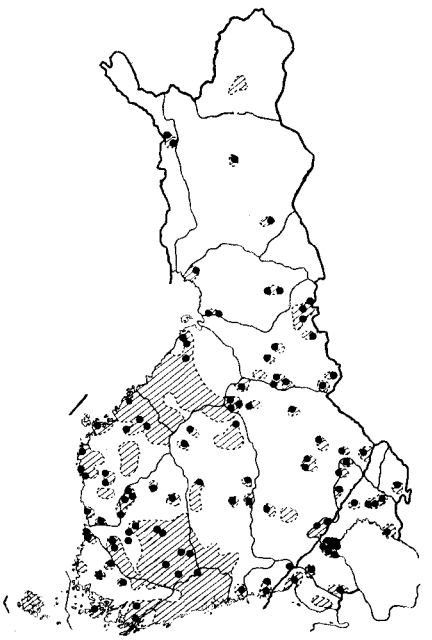

Fig. 11. Introductions of muskrats and the extent of their distributional area in the period 1928—32.

the direction of Riihimäki from the Puujoki river basin (p. 18). In the period 1931—33 the populations spreading westwards along the seashore occupied the region up to Snappertuna Commune and in 1934 they reached the Tammisaari area, which was simultaneously invaded by other muskrats from the direction of Tenhola, where an introduction had been made in 1929 (Korvenkontio, GRI). In the north, the muskrats met emigrants coming from the centre at Siuntio (date of introduction 1928). During this expansion, regions about 50—60 km. from the site of release (Heggesböle) were permanently settled.

D. The colonisation of the entire country and regional differences in the rate of dispersion

1. Range extension in 5-year periods

The range extension of the muskrats in Finland during the years 1927—57 is depicted in Figures 10—16.

By the year 1927 (Fig. 10), muskrats had been introduced into most water-system areas in Finland. The distribution was then usually restricted to the surroundings of the sites of release. In Pohjanmaa (Fig. 10, areas VII, VIII) and in the Kokemäenjoki drainage basin (IX) there were somewhat larger and more continuous populations.

In 1932, the picture was already greatly changed (Fig. 11) and, owing to further releases, far from uniform. Most of the new introductions (105) succeeded, hence the muskrats were distributed in numerous separate areas. In the earlier areas of introduction, extension of the range had taken place. Thus large areas were occupied in the northern parts of Pohjanmaa (VII), in the southern parts of Pohjanmaa (VIII) and in the Kokemäenjoki drainage basin (IX). In Uusimaa (XVI) the distributional area had likewise increased substantially. The only region devoid of muskrats was Kuusamo (IV), where no introductions had been made.

By 1937, a further new 137 introductions had been made. At this time, nearly all the separate populations in the western parts of Finland had been merged (Fig. 12). The more or less continuous distributional area comprised the major part of South-west and Central Finland but particularly in the eastern part of Central Finland there were still small areas from which the muskrat was absent (in areas VI, XI, XII, XIII). In North Finland enlargement of the disjunct areas had taken place. But in the Tornionjoki river basin (area II) the muskrat population had disappeared.

By 1942 (Fig. 13), the picture had again considerably changed, particularly in Central Finland. The areas VII—XVII were all occupied. The only areas from which muskrats were absent were in the Vuoksi drainage basin (XI) and in the Oulujoki drainage basin (VI), where there were two such areas, one in the east and the other in the central part. In the Simojoki and Kiiminkijoki river basins (V) the area occupied by muskrats had likewise grown considerably. Muskrats had been released in the Kuusamo water system (IV). Two successful introductions had also been made in the Tornionjoki drainage basin (II). The many different populations in the Kemijoki drainage basin (III) had merged, and new introductions had been made in 5 localities. On the other hand, the population introduced into Lapland (I) had obviously died out and a new introduction of 20 pairs of Canadian »tundra» muskrats did not succeed.

In the year 1947 (Fig. 14), the picture had hardly changed. In the Oulujoki drainage basin (VI) a slight expansion had occurred but in the eastern parts a recession had taken place. The muskrats had disappeared from the lower course of the Simojoki river basin (V). In Kuusamo (IV) two new introductions had been made and the populations in the middle reaches of the Kemijoki drainage basin had become continuous.

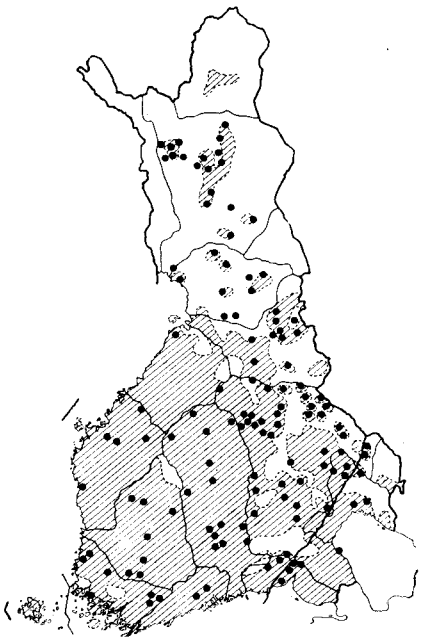

Fig. 12. Introductions of muskrats and the extent of their distributional area in the period 1933—37.

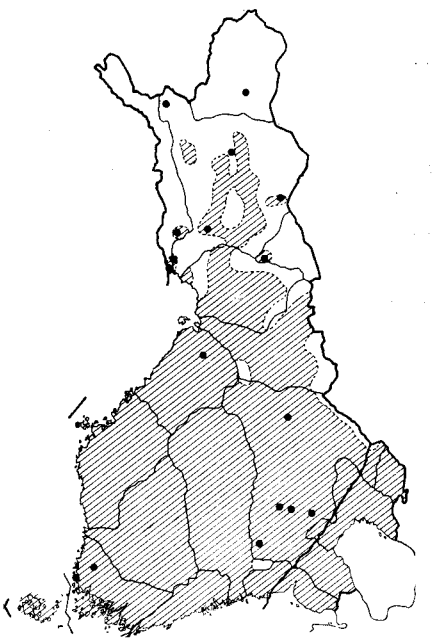

Fig. 13. Introductions of muskrats and the extent of their distributional area in the period 1938—42.

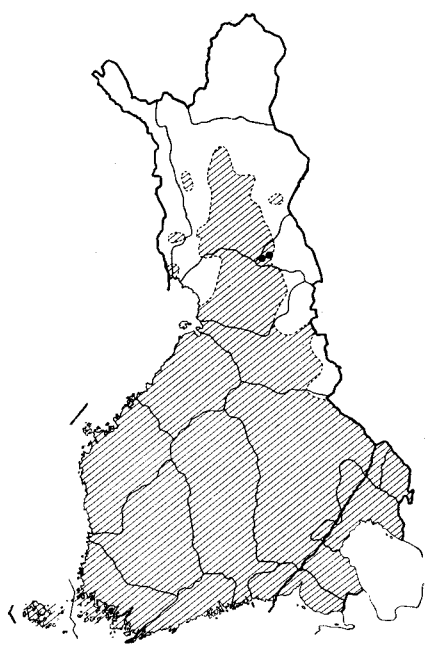

Fig. 14. Introductions of muskrats and the extent of their distributional area in the period 1943—47.

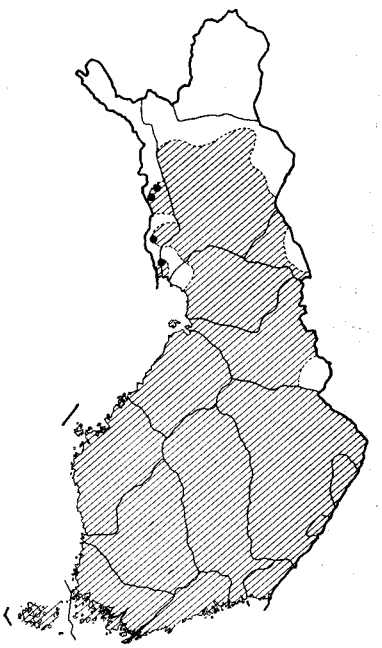

Fig. 15. Intruodctions of muskrats and the extent of their distributional area in the period 1948—52.

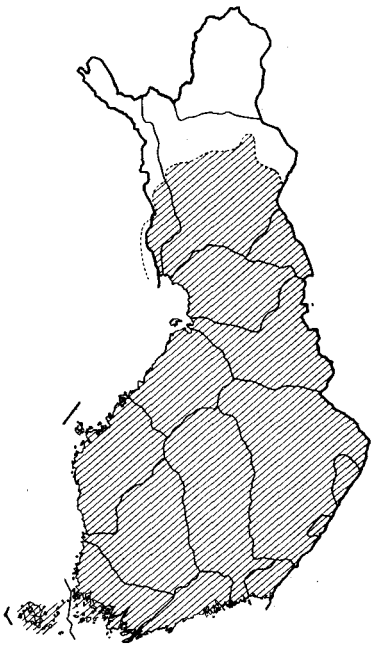

Fig. 16. The distribution of muskrats by the end of 1957.

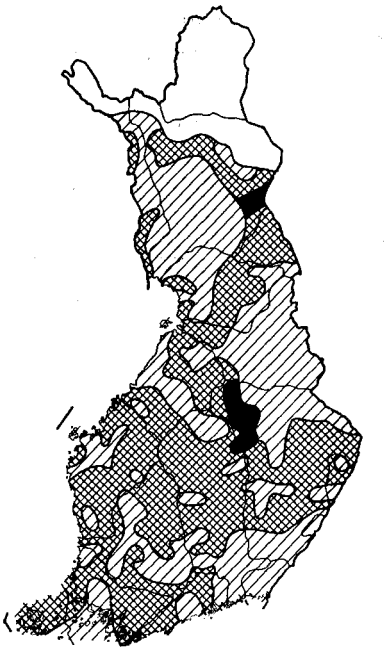

Fig. 17. The distribution of muskrats in 1958 and the density of populations in different parts of the country (black = population larger than average, cross hatching = average, open hatching = lower than average, blank = does not occur).

In the years 1952—57 (Figs. 15—16) the muskrats extended their area in North Finland. The greatest changes took place in the Tornionjoki and Kemijoki drainage basins (II, III). In the former, the area had likewise become continuous up to Pello. The muskrats spread from this region to the adjacent water systems in Sweden (Liljeström 1954, Velthyusen 1954, Lundberg 1955). Likewise the gap in the Oulujoki drainage basin and in the eastern parts of Kuusamo (IV) were filled up and Hailuoto was invaded.

Thus from the 293 sites of release in Finland, the muskrats spread in about 35 years (1920—55), until they occupied practically all those water systems where they could thrive. Probably the only further opportunity for expansion is in the drainage basin of Tornion—Muonionjoki (II.) Owing to the barrenness of the watershed area of the fjeld Saariselkä (areas I, III), muskrats can hardly spread naturally to the water systems of Arctic Lapland (I), where they have not become settled in spite of two introductions.

From the map of the present distribution of the muskrat (1958, Fig. 17) it can be seen that since the year 1957 (Fig. 16) the area of occupation has increased in North Finland. An extension of area has taken place in Muonio (in the area II), and in the upper course of the Kemijoki drainage basin (III) the population has reached somewhat further north. According to Brander (cf. Hoffmann 1958), the northernmost regions where muskrats have been found are lat. 67° N in the river Kemijoki and in the river Kaptugas, lat. 68° 30' N.

In 1955, the muskrat population in Finland was very abundant, but in the succeeding years it has steadily decreased. From the last inquiry (1958) addressed by the Game Research Institute to its observers (Fig. 17), it seems that the muskrat population is smaller than average locally in South and Central Finland, over a wide area in the Oulujoki drainage basin (VI) and in the upper course of the Vuoksi (XI). The muskrat population is also weak in the middle and upper courses of the Kemijoki (III) and in large parts of the Tornion—Muonionjoki river basin (II). Thriving muskrat colonies exist in two separate areas: in Salla Commune (III) and in the north-eastern corner of the Vuoksi drainage basin (XI). In all other places the muskrat population is of average size.

2. *Regional differences in the rate of expansion*

It has not been possible to obtain exact information on the size of the water areas occupied by muskrats in Finland during the successive periods, but if they are roughly estimated and plotted against the water areas available[1] the general picture is as in Fig. 18.

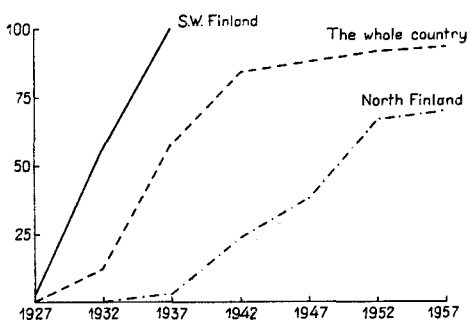

Fig. 18. The spread of muskrats as a percentage of the total area of watercourses.

[1] According to »Suomen pinta-ala kunnittain» (The areas of the Finnish communes) published by the General Survey Office (No. 27), Helsinki 1934.

The distributional area slowly increased throughout the country up to 1932. In the years 1933—37 the areas occupied were very large. On account of the numerous introductions and of favourable breeding conditions, over half the inland water areas of Finland became occupied. In 1938—42 expansion was still rapid, although clearly weaker than in the previous 5-year period. In the years 1938—42 the population density decreased noticeably (cf. Part V); the retardation in the expansion may largely be due to this fact. Thereafter the expansion was very clearly retarded. The occupation of the most barren upper courses of water systems and of the water systems in North Finland then continued slowly until recent years (Figures 14—17). In the water systems north of the Oulujoki river basin (area VI), the occupation has been distinctly slower than in other parts of Finland, especially southwest and south (Fig. 18). The slow dispersal of muskrats in North Finland where the first introduction was made as long ago as 1927, was obviously not caused by the small number of specimens introduced but by the generally infavourable conditions of this area.

In 1927, 3 pairs of muskrats were released in Lake Vuontisjärvi (I), obviously with success, since they increased in numbers and by 1930 they were already found at a distance of 21 km. from the site of release (Lehtola 1932). In 1937, the first specimens were found in Lake Inarinjärvi, about 100 km. from the site of release. The last reports of these muskrats were obtained in 1943 (H. Lehtola's letter of Jan. 28, 1947). After this, only reports of their absence have been received (GRI). The second introduction, this time of 20 pairs, was made in Lake Kirakkajärvi in 1939, but no muskrats have been seen in the region since that date (T. Mäki, verbal communication).

Seven introductions comprising altogether 35 pairs were made in the period 1930—51 in the Tornionjoki—Muonionjoki drainage basin (II). The first two made at Muonio, were unsuccessful (Figs. 11—12). The descendants of the remaining 29 pairs gradually released occupied the lower and central parts of the river system.

Releases of altogether 87 pairs of muskrats were made in the period 1931—39 in the Kemijoki river basin (III) in a total of 27 localities. In 20 of these the introductions are known to have succeeded.

In 1941 and 1943 15 muskrats were released in 3 localities in the waters of Kuusamo (IV). All these introductions succeeded.

In the years 1929—37, 14 introductions totalling 69 specimens were carried out in the area bordered by the Simojoki and Kiiminkijoki Rivers (V). Of these, only one was unsuccessful.

Altogether 374 specimens of muskrats were thus introduced into the water systems on North Finland (I—V) in 53 localities. Of these introductions 80 % were made before the year 1938 (Fig. 3, p. 12). There has thus been adequate time and material for expansion to have taken place.

The water systems in South and South-west Finland (areas IX, X, XV, XVI) were, on the contrary, invaded at a quite remarkable speed and were nearly completely occupied by the year 1937 (Fig. 12).

3. The emigration and spreading speeds in watershed areas of different types

There are reliable observations on altogether 53 cases of the point-to-point speed of emigration of single muskrat specimens in watershed areas of different types, 22 of them from coastal areas and 31 from inland. Unfortunately there are no reliable records from North Finland. These observations on the distances covered by single individuals are as follows[1]:

Rapidity classes	Coastal	Inland	Total
4—10 km./year	4	9	13
10—20 »	10	15	25
20—30 »	4	3	7
30—40 »	1	3	4
40—50 »	1	—	1
50—60 »	1	—	1
60—70 »	—	1	1
70—120 »	1	—	1
	22	31	53

From these data it can be seen that values of from 4 to 120 km. per year have been observed. Both in the coastal region with numerous rivers and in the water systems of the lake area, most reports reveal emigration speeds of 1—20 km. per year. Long-distance emigrations of scattered »pioneers», such as the emigration of muskrats from Ylivieska to Liminka (120 km. in a year, see above p. 14) and from Tuulos to Riihimäki (65 km./in a year, p. 17) are obviously rare events (see also Hoffmann 1958: 207—208). In the record case observed in Liminka floods probably caused passive spread and thus assisted the emigration. Observations made on the Karelian Isthmus by V. Ruokonen (verbal note) agree well with those of the present author. In the 1920's and 1930's emigration speeds of about 24—30 km. per year were observed there.

The large number of introductions obviously secured their success, but the number of muskrats released did not seem to have any noteworthy effect on the rate of emigration of single individuals. The emigration speeds of muskrats originating from the introduction of 200 pairs into Pieksämäki, for example,were almost equal to those of 29 individuals from Hauho—Tuulos or of 50 pairs from Virrat.

It might be anticipated that the speeds of emigration would be lower in the inland waters than in the river-dominated coastal areas, where the water systems are straighter. For during their wanderings muskrats generally explore every bight. No clear differences can be observed, however, between emigrations in these two types of water system.

[1] The distances were measured from a map (1 : 400.000) as carefully as possible, consequently along the shortest probable water system.

Nor is there any evidence of slower emigration upstream than downstream. The current as such thus seems not to have presented any hindrance to the invasion of our watercourses. In several cases, indeed, the emigration towards the lower course has been remarkably slow.

The occupation of the lower course and mouth of the river Kemijoki took an unexpectedly long time. Muskrats were already present in Tervola and in the Kaisajoki river, which is connected with the mouth of the Kemijoki in 1947 (Fig. 14), but the occupation of the latter did not occur until the year 1953. It is not known in detail whether it took place from the direction of the Kaisajoki river system, where muskrats were released in 1939 and in 1949, or from Tervola. The occupation of the mouth of the Simojoki river also took a long time. Muskrats had already become established in its upper courses in 1947 (Fig. 14) but the invasion of its lower course did not occur until 1953 (Fig. 16).

Ulbrich (1930) reported the mean speed of emigration of Central European muskrats to be 30—40 km. per year, i.e. distinctly higher than has been observed in Finland. Mohr (1933: 59) writes: »In the years 1923—24 in Bavaria the rate of migration is said to have amounted to 50—70 km. yearly». These values, like those given by Ulbrich (op.cit.), seem to be based on a rough estimation. According to Schilder (1956: 112), the mean distance covered per year (in 16 years) was 25 km. According to Turček (1957) in Slovakia the speed of emigration of muskrats was 20 km./year, and according to Hoffmann (1958:128) in Germany the distances covered were from 9 to 20 km./year as the crow flies. Because the favourable time for emigrations of muskrats (without snow and ice) is considerably longer in Central Europe than in Finland, the annual speeds of emigration should be higher in the former area.

A single marked male travelled 21.6 km. in a day and a female 10.4 km. in a day. Similarly in 15 days and nights one male had travelled 50 km against the current (= 3.3 km./24 hours, Pustet 1933).

From England, Warwick (1934) reports that in the period 1929—31, muskrats emigrated along the shores of Severn for a distance of 20 miles, i.e. at a rate of about 16 km./year. Between 1929—33, they had spread along the same river 9 miles upstream and 27 miles downstream, i.e. at a rate of 4—11 km./year. An isolated individual was found at a point near Oakengates, having travelled at a rate of about 13 km./year; others had wandered up the river Tern, at about 14 km./year, and to the upper course of Cound Brook, at about 15 km./year. In Scotland, muskrats had travelled a distance of 20 miles in two years (16 km./year). From Whitemoss Loch they emigrated to Dryburgh at a rate of about 24 km./year (in 1929—31) and to Glamis Castle (in 1933) at about 24 km./year.

The emigration speeds calculated from Warwick's data agree well with the values from Finland. From the Soviet Union, Lavrov (1931) mentions that in a short time the current carried muskrats scores of kilometres, even as much as 150 km./year. Novikov (1936 a) reports further that in autumn individual specimens may emigrate as much as 40—50 km and that, in barren watercourses in the Kola Peninsula (*idem* 1936 b) muskrats moved for distance of up to 70 km during

the fist year. These values, like the Central European record values (cf. above), agree well with the corresponding values from Finland.

Very little is known about speeds of emigration of other mammals. Kalela (1940) mentions that the polecat has extended its area in Finland in the years 1879—1939 by about 6 km./year. Gerschenson (1945) reports that in the Ukraine the black hamster (*Cricetus cricetus*) had increased its range during the years 1935—39 by as much as 150 km., or 38 km. per year. Ecke (1954) has established that in South Georgia the Norway rat (*Rattus norvegicus*) extended its area by about 20 miles as the crow flies in six years, i.e. by 5.4 km./year. According to Schilder (1956:112), in the Soviet Union the European hare (*Lepus europaeus*) has extended its range by about 18 km./year during the last 100 years.

These data show that the emigration of the muskrat has been very rapid in comparison with that of other mammals. In all the countries where the species has been introduced it has been observed that its range has increased remarkably quickly. It is, in fact, extraordinary that not even birds have been able to attain much higher rates of range extension. According to Schilder (1956:112) the starling (*Sturnus vulgaris*), which were introduced into North America, has there extended its range by 43—80 km./year.

The cumulative effect of trips beyond the home range is such that muskrats finally come to occupy all those watercourses which are suitable to them. The speed of their spreading varies very much in coastal and inland watercourses, as is seen from numbers of observations in the Table below, from 4 to 170 sq.km./year (areas of watercourses according to Sirén 1955):

Rate of expansion	Coastal	Inland	Total
4—15 sq.km./year	17	4	21
15—25 »	4	3	7
25—50 »	2	10	12
50—100 »	1	7	8
100—170 »	—	6	6
	24	30	54

In the river-dominated coastal areas the increase of area was 4 to 53 sq.km./year. The highest values (15—53 sq.km./year) are from areas where lakes are very numerous, as for instance in the following: Iijoki river basin (area V, Fig. 2, especially in its middle and upper courses, 1589 lakes, Olin 1936, representing 5.7 % of the area), Ähtävä river basin (VIII, percentage of lakes 10.6 %), Karvianjoki river basin (VIII, the middle and upper courses resemble the lake area of Finland, 6.0 %), Vuoksi river basin (X, 15.2 %, many large lakes, Olin 1936), Jänisjoki river basin (XII, 9.8 %, Olin 1936) and the Karjaan—Kiskonjoki river basin (XV, 10.2 %).

If we do not take into consideration the coastal watercourses resembling the Finnish lake area, the increase of area in the river-dominated coastal area has varied in most cases from 4 sq.km./year to 12.5 sq.km./year.

In the lake area of Finland the increase of area varied from 10 sq.km./year to 170 sq.km./year, the smallest values being from river-like watercourses in the coastal area where there

are few lakes. Examples of such areas are the river basin of Viiala (IX, lake percentage 6.7), the river basin of Loimijoki (IX, lake percentage 3.0), the watercourse of Jämsä (X, lake percentage 7.4) and the very barren watercourse of Valkeala (X, lake percentage 15.4).

The above data reveal that the rates of spreading were generally higher in the interior, in most cases 25 to 50 sq. km./year. The differences between the coastal and lake areas seem to be due to the fact that in river regions with few and small lakes a relatively larger proportion of the area constitutes the actual muskrat ecotope (Vité 1950) than in those areas where wide stretches of open water are virtually useless to muskrats. It is true that they sometimes swim across them, but the greater part of the lakes remain unoccupied. Hence, the greater the percentage of lakes in the watercourse, the greater is the apparent speed of spreading.

In order to eliminate from the calculations those areas which do not meet the requirements of muskrats, the author has counted the areas less than 1.2 m deep and covered with aquatic vegetation (Renqvist 1932) in the water systems in question. The computation was made from the formula presented by Renqvist (op. cit.): $k = 12.5 - {}^{j}/_{2}$, where k = the percentage of the area with aquatic vegetation and j = the lake percentage of the river basin. The values obtained are rounded values and give a rough indication of the area of the actual ecotope of the muskrats, comparable to the area of the littoral zone covered by aquatic vegetation.

On the basis of these values, the following entirely different values (numbers of observations) are obtained:

Rate of expansion	Coastal	Inland	Total
0.5—1.0 sq.km./year	13	3	16
1.1—2.0 »	8	7	15
2.1—3.0 »	1	10	11
3.1—6.7 »	2	10	12
	24	30	54

According to this calculation, the actual range extension would be 0.5 to 6.7 sq.km./year. Even so, the extension is more rapid in the coastal river-dominated water systems than in the lake areas of the interior. In most cases the increase varied from 0.5 to 2.0 sq.km./year on the coast, but in the interior the majority of observations gave values of over 2.1 sq.km./year.

The higher speed of expansion in the lake area may be explained in the following way: In the lake area the actual habitats of muskrats are restricted to suitable bays and bights rich in vegetation. In the large and medium-sized lakes, the strips of shore suitable for muskrats are often very limited and sparsely vegetated, especially if exposed to wind and waves. Limnologically they usually belong to the so-called dys-oligotrophic type. In such watercourses spread is rapid, because

the animals have to wander far afield to satisfy their food requirements and to find a mate (cf. Kalabukhov 1935: 234). According to Nikitina (1958), for instance, under poor food conditions the area per specimen of *Apodemus agrarius* was 2—6 times as large as when the amount of food was ample. In our barren water systems muskrats lead a very mobile life. In small bays, rich in vegetation, and in small lakes where enough food is available, the rate of population gain may be very rapid. If the populations become crowded, the offspring always have an opportunity to move to new areas. Our watercourses with their numerous rivers, brooks, lakes and pools are open biotopes. Spread is generally possible in all directions. On account of good opportunities to emigrate, the population increases as rapidly as the food situation permits. River banks, on the other hand, owing to their more homogeneous shore and aquatic vegetation, are capable of supporting muskrat populations for most of their length. Specimens spreading both upstream and downstream from the sites of release occupy the banks of rivers systematically. The centre of the area of introduction very quickly becomes overpopulated. Along a river emigration can take place in two directions only and is thus not so effective as in lakes. The regions already occupied are closed to the emigrants except right at the periphery, and the river systems thus represent more closed biotopes than the lake-dominated watercourses.

The small significance of the number of muskrats introduced on the speed of spreading is demonstrated by the following examples. In the watercourse of Rautalampi (area X), where altogether 208 pairs of muskrats were released, the rate of spreading was 127 sq.km./year. The percentage of lakes in the region is, however, unusually high (20.8 %) and if account is only taken of the waters near the shore, the rate of spreading was 5 sq.km./year, i.e. very rapid. In the area of Päijänne (X), however, only 6 pairs of muskrats were released, yet the respective rates of spreading were 130 and 5.5 sq.km./year. The rate of spreading was thus perhaps even more rapid in the latter case, whether reckoned per total water area or according to the area of the littoral zone. The number of muskrats introduced was likewise 6 pairs in the watercourse of Sysmä (X) and the respective speeds of expansion were 85 and 2.8 sq.km./year. In the northern parts of the Mäntyharju watercourse, 41 specimens were liberated, but the rates of expansion were nearly as great — 80 and 3.3 sq.km./year. These examples and many other similar cases from lakes of nearly similar dys-oligotrophic type, indicate that the numbers of specimens released shows no correlation with either the speed of spreading or the speed of emigration (p. 30). In view of this, cases in which only one pair was released are interesting. Such introductions were made in a total of 15 localities; 5 of them are with certainty known to have succeeded (Taivalkoski: Saarilampi, 1934; Suomussalmi: Kaivoslammet, 1930; Laitila: Tuulosjärvi, 1934; Mynämäki:

the lake of Nihattula, 1930; Nuijamaa: Kärkijärvi, 1935—37). Moreover, the observers reported the success of a further 8 introductions, but as muskrats simultaneously emigrated into the areas in question from elsewhere, these cases cannot be considered in detail here. Concerning the successful introductions of one pair mentioned above, the data regarding their fate are too inaccurate to permit of any computations.

The author has found few data on rates of spreading in the literature. Ecke (1954) reports that in South Georgia the Norway rat (*Rattus norvegicus*) spread over an area of 100 sq. miles in 6 years, i.e. at a rate of 4.3 sq.km./year. This value corresponds to the highest rate of expansion of the muskrat when only the littoral waters are taken in account. Jakowlew and Kolesnikov (1954) established that the black hamster had extended its range in the district of Rostov during the last decade by 200 sq.km., i.e. by 20 sq.km./year. This is a very high rate of expansion, but it corresponds well with the values obtained from Finland for muskrats if the entire area of the water systems is taken into consideration.

E. The poor survival of the introduced Virginian muskrat

The Virginian muskrat, or blue muskrat, *O. z. macrodon* (Merr.), of which about 300 specimens were introduced into 46 localities in Finland, has not become settled nearly so well as the nominate race. It was introduced into all the main water courses except those in Lapland (I), the Tornion—Muonionjoki river basin (II), the waters in Kuusamo (IV), the drainage areas in the northern parts of Pohjanmaa (VII), the water systems of Uusimaa (XVI), the Ahvenanmaa Islands (XIV) and the Suojoki river basin (XIII, Fig. 19).

According to data collected by the Game Research Institute, in 1944—45 the blue muskrat was common only in the near vicinity of the sites of release (Fig. 19). At the outlet of the Kokemäenjoki drainage basin there was a more extensive continuous population ranging from the surroundings of the town of Kristiina, from Parkano and Ikaalinen, through Karkku and Kiikoinen to Yyteri and further to the north-west corner of the water systems in S. W. Finland (XV, to Eura, Eurajoki, Loppi, Laitila). There was a second fairly continuous area east of Lake Pielisjärvi (area XI) and a third in Saimaa (XI) where it merged with the widespread population of the Kilpeenjoki River in the Viipuri district (XVII). A very heavy Virginian muskrat population existed in the latter area in the 1930's (Raekallio 1938).

By 1947—48 (Fig. 20), a clear decrease in the separate ranges of the blue muskrat populations could be observed. The more or less continuous area at the

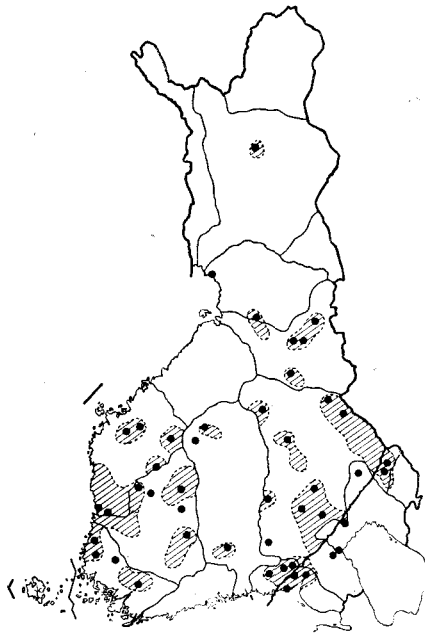

Fig. 19. The introductions of Virginian (blue) muskrats and their distribution up to the end of the year 1945.

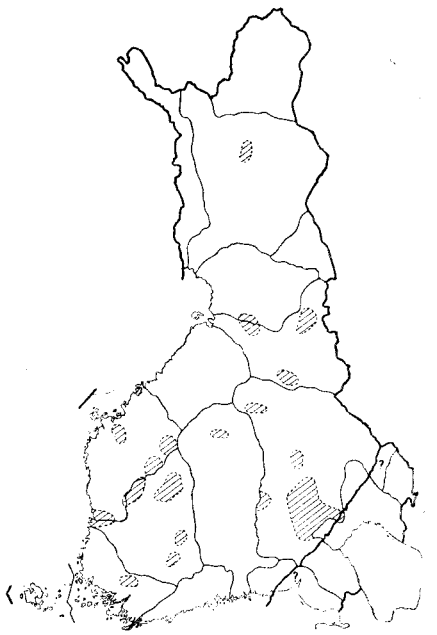

Fig. 20. The distribution of blue muskrats in 1948.

outlet of the Kokemäenjoki drainage area had been reduced to the area of Ahlainen—Noormarkku—Yyteri. The population east of Lake Pielisjärvi had disappeared. Only in the Saimaa district had the area occupied by the blue muskrat remained nearly as large as before.

From many localities of introduction the blue muskrats had totally disappeared or become mixed with the expanding brown populations. Crossing experiments (Smith 1938, Dozier 1948 a) have shown that the dark colour is a recessive character. In the fur trade, it is known that in regions where blue muskrats have been introduced, the quality of the pelt of brown (common) muskrats is better than in areas where the animals are of pure brown muskrat descent (cf. also Voipio 1948, 1950: 119—120).

Data obtained by the Game Research Institute concerning the distribution of blue muskrats in Finland indicate that a further reduction of their range occurred in the years 1950—53 (Fig. 21). In the Saimaa district the distributional area remained almost unchanged, but everywhere else the populations receded or even totally disappeared.

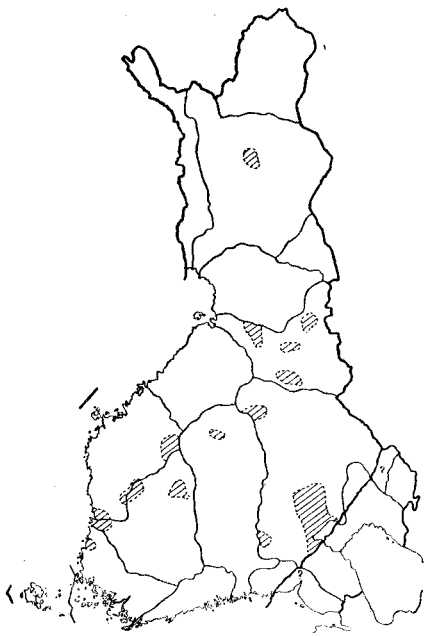

Fig. 21. The distribution of blue muskrats in 1953.

III. EXTERNAL FACTORS AFFECTING ACCLIMATIZATION

A. Climate

The muskrats introduced into Finland are either descendants of specimens from the northern parts of the range of the nominate race or of Central European muskrats of the same origin (p. 10). The Great Lakes area of North America is an excellent environment for the muskrats, and from this area the best pelts on the world marked are obtained (Hamilton 1939: 376, Gashwiler 1948).

According to Köppen's classification of climate (Köppen 1931:127, Connor 1938: 376) the central and northern parts of the range of the nominate race in America falls within the area of the climatic zone of humid-cold winters (Df). A boundary which coincides with the northern shore of the Great Lakes divides this climatic region into two types, a northern type (Dfc, the birch climate), where temperatures of over 10° C last for 1—4 months and where the mean temperature of the coldest month is over —38° C, and a southern type (Dfb, the oak climate), where the mean temperature of the warmest month is below +22° C but for at least four

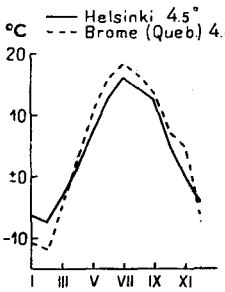

Fig. 22

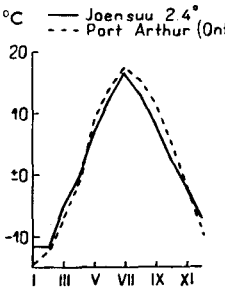

Fig. 23

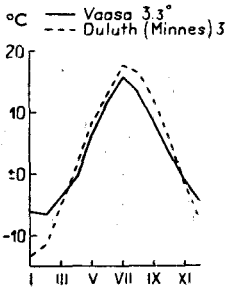

Fig. 24

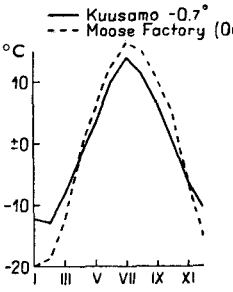

Fig. 25

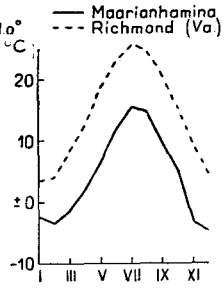

Fig. 26

Figs. 22—26. The annual mean temperatures and the annual course of the temperature at some North-American and Finnish observation stations.

months the temperature is over +10° C. The central parts of the range of the nominate race are in the latter region and in the zone with a temperate climate (Cf).

Finland possesses, for the most part, the same type of climate as the northernmost parts of the area of the nominate race, namely the Dfc-type. Only the southwest corner of Finland and the Ahvenanmaa archipelago belong to the Dfb-type. The main range of the Virginian or blue muskrats in their native country, on the other hand, is situated in an area with quite a different type of climate (Cf) such as prevails in Central Europe but does not occur in Finland at all.

In the following a comparison is made between the temperature conditions of certain parts of the native area of the nominate race (according to Ward & Brooks 1936, Connor 1938), and Finnish observational stations (Keränen 1946) where the annual mean temperature is about the same.

The very similar course of the temperature curves in the different months of the year can be observed from Figures 22—25. In the Finnish observation stations the temperature seems to be a little lower in the summer and a little higher in the winters.

In the native area of the blue muskrats (Fig. 26) the temperature is consis-

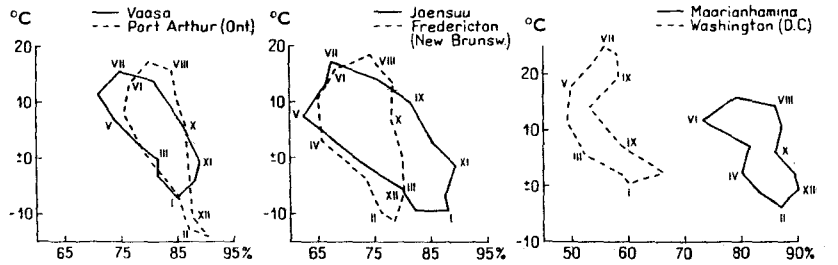

Fig. 27 Fig. 28 Fig. 29

Fig. 27. Temperature and relative humidity in different months of the year in Vaasa, where the annual mean temperature is 3.3° C and average relative humidity 82 %, and in Port Arthur, where the corresponding values are 2.3° C and 83 %.

Fig. 28. Temperature and relative humidity in different months of the year in Joensuu (Niittylahti), where the annual mean temperature is 2.4° C and average relative humidity 78 %, and in Fredericton, where the corresponding values are 4.7° C and 74 %.

Fig. 29. Temperature and relative humidity in different months of the year in Maarianhamina, where the annual mean temperature is 5.1° C and average relative humidity 83 %, and in Washington, where the corresponding values are 12.6° C and 56 %.

tently higher than the temperature of the Finnish locality (Maarianhamina) where the annual mean is highest.

In Ohio, from where the muskrats were imported to Central Europe, the annual mean temperature on the shore of Lake Erie is clearly higher (9,6° C) than in any Finnish observation station but corresponds well with the values for certain European stations (e.g. in the Prague area, Czechoslovakia, one of the sites of release, the annual mean is 9.2° C, Alt 1932).

The climographs of temperature and humidity of the original range of the nominate race are very similar to those of this country (according to the Meteorological Office). The climographs of Vaasa and Port Arthur (Fig. 27), for instance, overlap to a substantial degree. In midsummer, however, Vaasa is cooler and drier than Port Arthnr, whereas in midwinter Port Arthur is consistently colder. Great similarity is also shown by the climographs of Joensuu and Fredericton (Fig. 28). In the former, however, the autumns and winters are clearly more humid than in the latter.

In the climograph for a native locality of blue muskrats (Washington D.C.) the humidity and temperature values do not correspond at all to the values for Maarinahamina (Fig. 29).

Some of the climographs based on temperature and precipitation values from the native range and from Finnish observational areas (Korhonen 1952) show conspicuous differences. The annual precipitation is heavier in the region of the Great Lakes than in Finland (about 750 versus 620 mm., the latter refers to the southern and central parts of Finland, in North Finland the corresponding value is 520 mm.). The climographs of Sodankylä and Moose Factory correspond well with each other

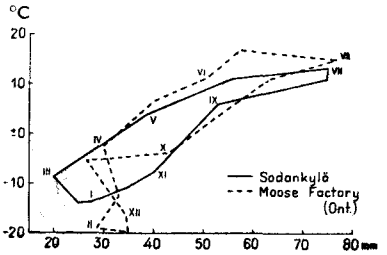

Fig. 30. Temperature and precipitation in different months of the year in Sodankylä, where the annual mean temperature is —1.2° C and annual precipitation 520 mm., and in Moose Factory, where the corresponding values are —1.0° C and 520 mm.

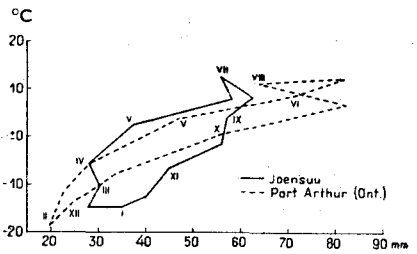

Fig. 31. Temperature and precipitation in different months of the year in Joensuu (Niittylahti), where the annual mean temperature is 2.4° C and annual precipitation 585 mm., and in Port Arthur, where the corresponding valuesare 2.3° C and 595 mm.

(Fig. 30), whilst in Port Arthur the late summer and winter are more rainy than in Joensuu (Fig. 31), and in Heron Bay the winter and summer are wetter than, for instance, in the town of Kajaani (Fig. 32). The winter is also somewhat colder in the American station.

In Finland the south-west corner of the country is characterized by relatively warm summers and mild winters, and the humidity is relatively high. A comparison of the climographs for temperature and humidity of a native locality of the blue muskrat, Richmond (Va), with the corresponding values for Maarianhamina, S.W. Finland, shows that these localities are entirely different (Fig. 33).

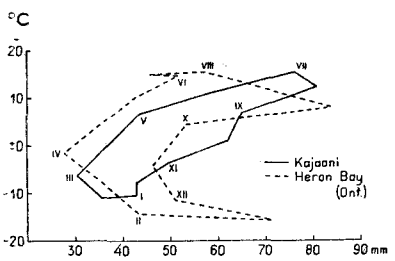

Fig. 32. Temperature and precipitation in different months of the year in Kajaani, where the annual mean temperature is 1.3°C and annual precipitation 627 mm., and in Heron Bay, where the corresponding values are 2.2° C and 616 mm.

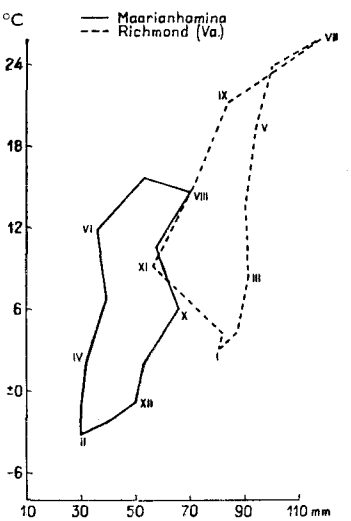

Fig. 33. Temperature and precipitation in different months of the year in Maarianhamina, where he annual mean temperature is 5.1° C and annual precipitation 558 mm., and in Richmond, where the corresponding values are 14.3 ° C and 1067 mm.

The great similarity between the climates in this country and in the native area of the nominate race in the northern parts of North America is one of the fundamental reasons for the success that has attended the introduction of this race into Finland. On the other hand, the poorer survival of the Virginian muskrats is understandable, because the native area of this race is situated in a climatic region differing in many respects.

B. Variations in water-level

In the North American area of the nominate race, the precipitation changes considerably in the direction from east to west. In Toronto, for instance, annual precipitation is 808 mm. and in Port Arthur only 593 mm. Their amounts are perhaps not so important as such, but the fact that they are distributed equally over the different seasons is relevant in this connection, because great floods and long periods of drought are avoided. Hundreds of thousands of muskrats were drowned in the spring of 1927, for instance, when the Mississippi flooded to the muskrat regions in Louisiana (Hodgson 1927, cf. also Errington 1937 a, 1939 a, 1940). It has been established that muskrats thrive best in watercourses where the variation in the water-level is small (e.g. Smith 1938, Bellrose & Brown 1941, Bellrose & Low 1943, Gashwiler 1948, Bednarik 1956, etc.).

The rate of discharge of rivers in Finland generally decreases during the first three months of the year and is annually at a minimum before the melting of the snow, but the water-level then continues to rise until June. An abrupt reduction then begins and continues till October (in North Finland to September), but the autumn rains then cause a rise of the water-level. Yet it does not reach the spring maximum and in November the slow fall typical of the winter period begins again.

In those areas where the percentage of lakes is comparatively high, the spring flood is delayed and the yearly variations are not so great. Thus the difference between mean high and mean low water is only about 0.7—1.0 m. In districts with few lakes (in coastal areas) the spring and autumn floods are noticeably higher (Renqvist 1952).

The annual variations of the water-level and other hydrographic conditions in our watercourses, and particularly in the entire lake district of the interior are very similar to those in the native areas of the muskrat. As the normal annual fluctuations in the water-level of the Finnish watercourses are usually small and slow, they do not present any threat to the survival of muskrats. This is seen from the fact that the introduced animals became established both in the watercourses of Pohjanmaa, where widespread annual flooding is the rule, and in the lake district where the autumn and spring floods are considerably less extensive.

The effect of the fluctuation of the water-level upon the muskrats can also be studied in certain coastal areas of Finland. Tidal changes of the water-level are

negligible (cf. e.g. Jurva 1952), but there are annual changes caused by other factors. The following regular changes can be observed: Twice a year (at the end of December and beginning of January and in August and September) there is high water; low water prevails in May and throughout the autumn. At the heads of the Gulf of Finland and the Gulf of Bothnia the greatest deviations from the mean water-level may amount to as much as 1.5 m (Jurva 1952). Since in these regions the coast is very unfavourable to the muskrats (wide, shallow waters along the shore, hard bottom, littoral zone extending by as much as one kilometre from the coast line, paucity of aquatic vegetation), such variations have a very adverse effect on the muskrat populations, particularly because they may occur in the course of some hours. The shallow waters in question are liable to freeze hard and, because there is no protecting archipelago, are also exposed to storms and surf.

For these reasons the areas in question are not suitable localities for muskrats (cf. pp. 14—17). The coastal areas at the heads of the Gulf of Finland and the Gulf of Bothnia have proved effective barriers to the spread of the animals. It has not been possible to detect any emigration along these coasts. From the other coastal areas, on the contrary, there are many observations of emigrations taking place along the seashore (pp. 23—24).

C Biotopes and food

1. Occurrence of muskrats in watercourses of different types

The wide range of the muskrat and its racial differentiation are good indications of its ecological adaptability. Muskrats have been established virtually to live: »From beaver pools in mountain streams to desert waterholes, glacial marshes to irrigation seepages, river bayous to brooks, ditches and lakes . . .» (Errington 1951: 274) and »It finds optimum living conditions in places where heavy growths of herbaceous vegetation occur in close proximity to still or sluggish water that fluctuates neither suddenly nor greatly in depth» (Errington 1939 a: 168—169).

In spite of the great adaptability of the muskrat to the most varied watercourses, its success is often determined by certain environmental factors.

a. Plant productivity

According to American investigators, lakes and ponds form one of the main biotopes of the muskrat. During the years 1946—49, the present author made an estimate, based on winter houses, den burrows and other signs (see Lay 1945,

Table 1. The numbers of muskrats in eutrophic and dys-eutrophic lakes in the Kokemäenjoki drainage basin.

No.	Commune, lake	Area ha.	Average depth m.	Length of shore-line km.	Aquatic vegetation		No. of winter houses and/or den burrows					
					Area ha.	% of area	1946/1947	1947/1948	1948/1949	Average	Aquatic vegetation ha.	Length of shore-line km.
1.	Kangasala, Kirkkojärvi	165	2.0	7.2	19.3	11.7	25	18	26	23	1.2	3.2
2.	» Ahulinjärvi	48	2.0	4.4	19.6	41.4	24	21	22	22	1.1	5.1
3.	» Säkkölänjärvi	26	1.0	2.3	11.2	43.1	11	14	8	11	1.0	4.9
4.	» Kyläjärvi	11	1.5	1.3	4.8	47.2	5	6	5	5	1.1	4.1
5.	» Nuorronjärvi	20	2.5	1.9	7.2	37.5	12	13	7	11	1.5	5.6
6.	» Heposelkä.....	210	5.0	13.3	49.0	23.3	30	32	48	37	0.7	2.8
7.	» Raikkujärvi	35	3.0	3.6	3.7	10.1	2	3	2	2	0.6	0.6
8.	» Taivallampi	16	1.0	1.7	15.6	100.0	34	25	30	30	1.9	17.5
9.	» Ihari	17	0.5	3.3	15.6	91.8	10	9	5	8	0.5	2.4
10.	Kuhmalahti, Puntarinlahti ..	75	1.5	5.6	15.0	20.0	20	22	27	23	1.5	4.1
11.	» Tervajärvi	74	1.0	5.0	54.0	73.2	28	21	26	25	0.5	5.0
12.	Lammi, Lovojärvi	6	7.0	1.5	1.5	25.9	3	2	2	2	0.9	1.5
13.	» Lampellonjärvi	7	3.0	1.4	2.0	29.8	4	1	3	3	1.4	1.2
14.	Suodenniemi, Valkeajärvi	10	3.0	1.5	1.1	11.0	1	1	2	1	1.2	0.9
15.	» Kirkkojärvi	71	3.5	6.4	12.3	17.4	9	10	15	11	0.9	1.8
16.	» Koivuniemenj...	46	1.0	4.5	32.4	71.2	18	19	13	17	0.5	3.7
17.	Mouhijärvi, Mouhijärvi	692	3.9	22.0	76.0	11.0	30	45	49	41	0.5	1.9
18.	Kiikoinen, Kuorsumaanj.	252	1.5	7.7	66.5	26.5	115	120	145	127	1.9	16.5
19.	» Marjajärvi	311	0.5	8.5	311.0	100.0	80	45	15	47	0.2	5.5
20.	» Kiikoisjärvi (N. part)	168	3.5	7.4	20.7	12.3	40	42	27	36	1.8	4.9
21.	Ikaalinen, Sarkkilanjärvi	23	2.0	2.6	7.2	31.0	6	8	4	6	0.6	2.3
22.	Tyrvää, Liekovesi	448	4.0	16.5	95.0	21.2	250	258	150	219	2.3	13.3
23.	Kauvatsa, Puurijärvi	445	0.5	13.0	445.0	100.0	125	275	243	214	0.5	16.5
24.	Urjala, Kivijärvi	74	1.2	4.4	21.6	29.4	25	50	28	34	1.6	7.8
	Σ	3250	2.3	147	1307	40.2	907	1060	902	956	0.7	6.5

Dozier 1948 b, Artimo 1949, 1952, Bellrose 1950) in the region of the Kokemäenjoki basin, of the numbers of muskrats in 48 lakes of different types (*sensu* Järnefelt 1952).

Of the lakes investigated 24 were eutrophic and dys-eutrophic lakes (Table 1) with a total area of 3250 hectares. The aquatic vegetation was rich in species and its growth luxuriant. Approximately 40.2 % of the water area was found to be covered with aquatic vegetation. By this the author means the zone extending from the shore line to the outer limit of the farthest hydrophytes and the floating vegetation. The submerged aquatic plants possibly present outside the area were not taken into consideration. However, since the zone of vegetation most frequently extends to depths of 1—1.5 m. (see p. 33) the area calculated in this way

Table 2. The numbers of muskrats in dystrophic lakes in the Kokemäenjoki drainage basin.

No.	Commune, lake	Area ha.	Average depth m	Length of shore-line km.	Aquatic vegetation		No. of winter houses and/or den burrows					
					Area ha.	% of area	1946/1947	1947/1948	1948/1949	Average	Aquatic vegetation ha.	Length of shore-line km.
25.	Kiikka, Kivijärvi	30.0	4.0	3.6	7.8	26.0	3	2	2	2.3	0.3	0.6
26.	» Tyrisevä	47.0	5.5	4.5	6.2	13.2	2	3	2	2.3	0.4	0.5
27.	Kauvatsa, Lievijärvi	138.0	1.5	10.8	46.7	33.8	21	25	20	22.0	0.5	2.0
28.	Ikaalinen, Kotkatjärvi	3.0	1.0	1.0	2.7	76.7	3	2	2	2.3	0.9	2.3
29.	» Teejärvi	14.0	2.0	2.9	2.9	20.6	3	3	2	2.7	0.9	0.9
30.	Parkano, Peräjärvi	24.0	3.5	3.5	7.8	32.1	2	3	2	2.3	0.3	0.7
31.	» Pitkäjärvi	7.4	4.0	2.4	1.4	18.9	0	0	0	0	0	0
32.	Kangasala, Linnajärvi	45.6	7.0	5.0	4.5	9.9	3	4	3	3.3	0.7	0.7
33.	» Koskijärvi	7.4	2.5	1.4	3.0	40.5	2	3	2	2.3	0.8	1.6
34.	» Vähäjärvi	5.2	3.0	1.0	0.5	9.0	0	0	0	0	0	0
35.	Loppi, Pitkälampi	4.4	3.0	1.2	0.6	13.6	0	0	0	0	0	0
36.	Lammi, Saarisjärvi	12.5	5.0	2.0	1.8	14.4	1	1	1	1.0	0.6	0.5
37.	» Särkijärvi	1.8	2.0	0.4	0.4	20.8	0	1	0	0.3	0.8	0.8
38.	» Iso-Mustajärvi	2.9	3.0	0.9	0.5	17.2	0	0	0	0	0	0
39.	» Kaitalampi	2.3	2.0	0.8	0.8	34.8	1	1	1	1	1.9	1.5
40.	» Hautajärvi	7.5	6.0	1.2	1.2	16.0	1	1	1	1	0.8	0.8
	Σ	353	3.2	43	89	25.2	42	49	38	43	0.5	1.0

will correspond to the actual habitat of the muskrats (cf. p. 33). In the eutrophic and dys-eutrophic lakes investigated, the region comprised a total of 1307 ha.

In the eutrophic lakes the population density was highest. In these, 0.2—2.3 (average 0.7) houses were found per hectare of aquatic vegetation. It is to this type of vegetation that the North American »muskrat marshes and swamps» belong and they may be said to correspond to our shallow eutrophic lakes nearly filled up with vegetation (oral information by J. Koskimies, Assistant Professor of Zoology). There such biotopes provide the best habitats for muskrats. Korvenkontio (1925: 23) and Bachrach (1930: 109) report that, according to the biological survey of muskrats carried out by the U.S. Departement of Agriculture, 500 acres of good natural muskrat marsh yields about 2500 pelts, or 5 pelts per 0.4 hectare, annually. Hewitt reports (according to Trippensee 1953: 133). that an average of 7 muskrats per acre have been trapped on a 1.200-acre marsh in western Ontario, and states that a good marsh should yield 6 to 8 rats per acre (0.4 ha.) annually

The number of dystrophic lakes investigated amounted to 16 (Table 2). They were mostly smaller than the eutrophic or dys-eutrophic lakes and their total

Table 3. The numbers of muskrats in oligotrophic lakes in the Kokemäenjoki drainage basin.

No.	Commune, lake	Area ha.	Average depth m.	Length of shore-line km.	Aquatic vegetation		No. of winter houses and/or den burrows					
					Area ha.	% of area	1946/1947	1947/1948	1948/1949	Average	Aquatic vegetation ha.	Length of shore-line km.
41.	Loppi, Salmijärvi	24.0	4.5	3.6	3.0	12.5	0	0	0	0	0	0
42.	» Kalattomanlammet	12.4	5.0	2.7	0.5	4.0	0	0	0	0	0	0
43.	Kalvola, Lunkinjärvi	125.0	3.5	7.8	7.8	6.2	3	2	1	2	0.2	0,3
44.	Kuhmalahti, Pentojärvi	34.4	3.0	5.3	2.1	6.1	0	0	0	0	0	0
45.	Lammi, Huhmari	1.6	5.0	0.4	0.1	4.7	0	0	0	0	0	0
46.	» Valkea-Mustajärvi	13.2	3.0	2.1	2.2	16.7	0	0	0	0	0	0
47.	» Syrjänalunen	0.9	3.0	0.6	0.1	4.4	0	0	0	0	0	0
48.	Kuorevesi, Heräjärvi	7.0	3.5	1.2	0.1	0.4	0	0	0	0	0	0
	Σ	218.5	3.8	23.6	15.8	7.2	3	2	1	2	0.1	0.01

area was 353 hectares. The area covered by aquatic vegetation was relatively smaller, on an average only 25.2 % of the total water area, comprising 89 ha.

The population density of muskrats was 0—1.9 (average 0.5) houses per hectare of aquatic vegetation. The reason for the lower population density was obviously the lower plant productivity. In many dystrophic lakes muskrats evidently thrive and the population densities may be as high as in the eutrophic lakes (for instance Kotkatjärvi 0.9, Teejärvi 0.9, Linnajärvi 0.7, Koskijärvi 0.9). On the shallow shores of the lakes in question the aquatic vegetation may even become fairly luxuriant. The 4 dystrophic lakes investigated (Pitkäjärvi, Vähäjärvi, Pitkälampi and Iso-Mustajärvi) were, however, totally devoid of muskrats. In these typical woodland lakes the aquatic vegetation was rather sparse.

From North America there are no reports of the occurrence of the nominate race in dystrophic lakes, although these are evidently the prevailing type of lake in the northern parts of its range. Concerning the race *O.z. spatulatus* (Osgood), however, Osgood (1901: 66) points out that in Alaska it is »rather common about small ponds in the peat bogs near Tyonek.»

There were only 8 oligotrophic types among the lakes investigated (Table 3), for lakes of this type are very rare in the Kokemäenjoki drainage basin. The total area of these lakes was 219 ha., and the area of the aquatic vegetation was only 16 ha. i.e. 7.2 % of the total area of the lakes.

Muskrats were observed in only one of these oligotrophic lakes. They are so poor in vegetation that they cannot generally support a muskrat population

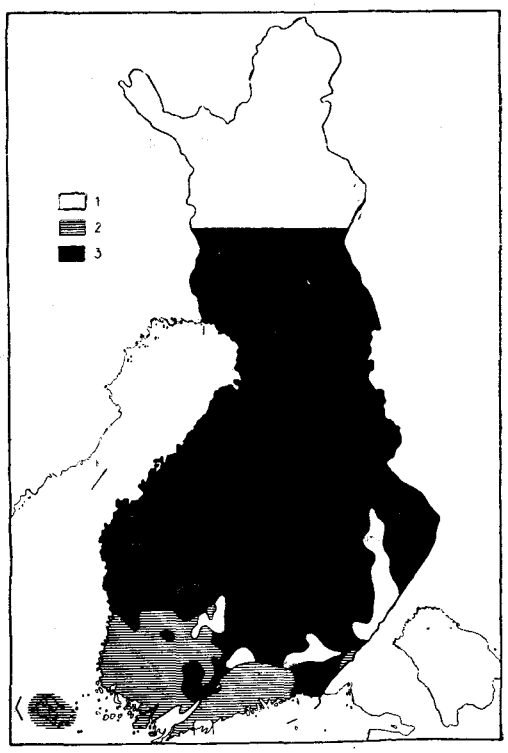

Fig. 34. The regional distribution of lake types. — 1 = oligotrophic, 2 = eutrophic and dys-eutrophic, 3 = dystrophic. According to Järnefelt 1952.

throughout the year. Signs of the temporary presence of muskrats were noted in autumn, but overwintering has never been observed.

Concerning the ability of the nominate race to succeed in oligotrophic watercourses, the author has found no data in the American literature. Of the race *O.z. osoyoosensis* (Lord) Dalquest (1948: 361) mentions that it occurs: »in contrast to the marsh-occupying muskrats, along the open, marshfree shores of the lake in deep clear water where waves lap the shore. These muskrats live exclusively in burrows dug in the banks and feed upon freshwater mussels.» The races living in northern parts and mountains have also become adapted to life above the tree zone even in lakes and pools of the tundra regions (cf. Osgood 1900, Borel & Ellis 1934, Porshild 1945, etc.). Such watercourses are often of oligotrophic type.

In Finland the most productive watercourses which offer the best conditions for muskrats, prevail in S. and S.W. Finland (see Fig. 34). Elsewhere dystrophic types are characteristic up to the Arctic Circle; still further north the oligotrophic watercourses predominate. Oligotrophic lakes occur, in addition, here and there in esker country and in rocky areas in various regions. In Lapland, where such

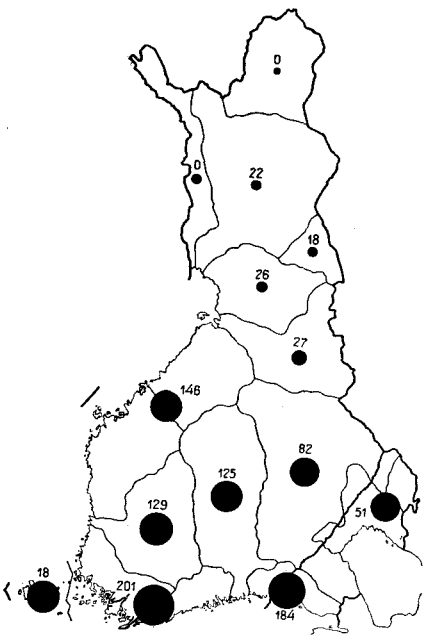

Fig 35. The ratio of agricultural and of so-called public areas in % of the area in different water-system areas (black circles according to Ilvessalo 1929: 86). The numbers indicate the average muskrat catches per sq.km. covered by aquatic vegetation in 1946—52.

lakes predominate, the introduced muskrats have not become established (Enontekiö, Inari). Not until recently have they extended their range as far north as Muonio (p. 28). The northern limit of the permanent range of the muskrat in Finland (cf. Figs. 17 and 34) approximately coincides with the zone where the proportion of dystrophic lakes decreases in favour of oligotrophic ones.

The productivity of a watercourse is closely depended on the environment. In the watercourses affected by cultivation and settlement, the aquatic plant productivity is comparatively high. This depends both on the fact that the settlers choose the most fertile land in the first place, and that their agricultural and other activities have a fertilizing effect. Thus the highest densities of muskrat populations are reached in the eutrophic watercourses situated in the regions where intensive cultivation is practised. The highest catches are, of course, also made in these areas (Fig. 35).

It was already established (pp. 28—29) that the rate of expansion of the muskrat populations was clearly higher in South than in North Finland. One of the reasons for this is very likely the better food supply in the eutrophic watercourses of the southern parts of the country. In the northern water systems of low pro-

ductivity, shortage of food obviously prevented the increase of the muskrat populations and thus slowed down the rate of their expansion.

b. Depth

It has been established above that the ecotope of muskrats is the more or less narrow, shallow shore zone. Both the area of the vegetation and the numbers of muskrats depend on its extent. In shallow lakes the area covered by plants is generally relatively larger than in deep ones. The eutrophic lakes investigated (Table 1) were mostly shallow (medium depth 2.3 m.), the dystrophic ones (Table 2) deeper (3.2 m.) and the oligotrophic ones (Table 3) deepest (3.8 m.). When the number of muskrat houses relative to the length of the shore-line was computed, the highest values were obtained for the lakes where the littoral zone was widest. Examples among the eutrophic lakes (Table 1) examined were Taivallampi (with 17.5 houses/km. of shore-line), Kuorsumaanjärvi (16.5/km.), Puurijärvi (16.5/km.) and Liekovesi (13.3/km.). In the other eutrophic lakes the number of houses was 0.9 to 7.8 houses/km. (mean 6.5). In dystrophic lakes (Table 2) the values were decidedly lower, 0 to 2.3/km. and in oligotrophic ones still lower (Table 3). Even in dystrophic lakes the highest values occurred in the shallower lakes: in Lievijärvi (2.0/km.) and Kotkatjärvi (2.3/km.).

Among the eutrophic lakes investigated, however, there were some in which the density of muskrats was very small in relation to the area of the vegetation. In these watercourses (Ihari, Tervajärvi, Koivuniemenjärvi, Marjajärvi, Puurijärvi) the mean depth was also smallest of all. They were evidently too shallow. During severe winters, especially, they froze to the bottom and the survival of the muskrats was threatened (cf. Aldous 1947, Bellrose 1950). It is for this reason that in Finland such shallow, drained lakes or bays are generally not especially favoured by muskrats in spite of the ample supply of food.

An example of such a lake is Marjajärvi in Kiikoinen (No. 19, Table 1). The area of this lake, which was in process of being drained, was 311 ha. and the maximum depth about 1 m. (1945). The vegetation (*Scirpus, Typha, Phragmites, Equisetum*, etc.) was very dense and luxuriant. In the winter of 1945/46 there were 35 muskrat houses, in 1946/47 80 in 1947/48 45 and in 1948/49 only 15. By October 1950 the muskrats had evidently abandoned the lake, which was drained nearly dry.

In the dys-eutrophic lake Puurijärvi in Kauvatsa (No. 23, Table 1) the depth and aquatic vegetation are similar (cf. Kalela 1938), but there is a permanent current of water along the floatway. The lake has at all times supported a large muskrat population. In the winter of 1946/47 there were 125 houses, in 1947/48 275 and in 1948/49 243. In October 1950 there were 190 houses. The density of muskrats is not so high, however, as is usual in eutrophic lakes. It is only 0.5 per hectare, or the same as the average for dystrophic lakes. In this shallow lake the muskrats are obviously very sensitive to the relatively small variations of the water level and therefore the fluctuations in population densities in different years are very great. Similar

cases are known from North America, where it has been found that effective ditching of a productive muskrat marsh for mosquito control is definitely injurious (Stearns, McCreary & Daigh 1939, 1940).

Muskrats also readily established themselves in small pools and artifical ponds, which are usually shallow and have luxuriant vegetation. Thus, for instance, the stretches of water, rich in vegetation, which have become cut off from the River Vantaa in the district of Riihimäki have proved to be very productive habitats of muskrats. Although the aquatic vegetation of these pools is plentiful enough to guarantee food throughout the year, muskrats move from them back to the river itself in autumn, obviously because these localities without water currents may become frozen throughout (cf. Errington 1937 d, Hamerstrom & Blake 1939).

As in the native country of the muskrat (e.g. Lantz 1926, Anthony 1935, Grenwell 1948, Odum 1949), fish culture ponds have proved to be suitable localities in Finland also. They often have a luxuriant vegetation and the water level is kept nearly stable. The amount of water is also so ample that the ponds cannot freeze to the bottom in winter. For instance, muskrats have continuously occupied the ponds of the Porla Fish Cultivation Station, where they settled immediately after their arrival at Lohjanjärvi in 1932 (e.g. Hakola 1931, Valli 1931, Brofeldt 1934).

Muskrats have often colonized the shallow, richly vegetated ponds forming in clay-pits or mud-pits. In Ilmajoki Commune in Pohjanmaa they usually live in such biotopes and thrive in them better than in the nearby river, to which, however, they retreat for the winter when the shallow ponds freeze to the bottom (I. Lahti, M. Rintala, GRI). Similar observations were reported by A. Forsell (GRI) from Toijala. Karpukhin (1958) reports that in the region of the River Kolyma in Siberia, muskrats are destroyed in the shallow lakes in winter. In such lakes they generally move further from the shore and construct their winter houses direct on the ice.

In deep lakes with steep shores the littoral zone and the area covered by vegetation are very narrow. Thus in the eutrophic Raikkujärvi (No. 7, Table 1) the population density remained small (0.6 houses/km.) and for the same reason in Lake Valkeajärvi (No. 14) the numbers were very low (0.9). The absence of muskrats from four dystrophic lakes (Nos. 31, 34, 35, 38, Table 2) can probably be explained in the same way.

c. Nature of the shores

Muskrats dig their bank leads and den burrows in the banks of shores. The structure of the bank must thus, on the whole, be such as to permit digging. Rocky and stony banks, and even banks of pure sand are unsuitable for digging and therefore not well fitted to harbour muskrats.

Only if the population density is very high can the muskrats live in small holes dug under littoral stones on stony shores, such as were described by Korvenkontio from the islands of Längelmävesi (cf. p. 19). No similar observations have been made latterly (oral statement of the game warden, O. Heino) nor has the author been able to observe any such dens in the region in question.

The low population density in certain lakes examined by the author obviously has the same cause. Thus the population density in the eutrophic Lake Raikkujärvi, with its steep and narrow shores, was very low (0.6/km. of the shore-line and 0.6/hectare area covered by aquatic vegetation). The entire southern shore of the lake (half the shore-line) is rocky and gravelly and there are no muskrats there. The situation is similar in Valkeajärvi (0.9/km.), and Mouhijärvi (1.9/km.), both with parts of the shores obviously uninhabitable. In the dystrophic lakes Pitkäjärvi, Vähäjärvi, Pitkälampi and Iso-Mustajärvi (Table 2) the reason for the absence of muskrats is, besides the narrowness of the littoral zone, the wide and quaking peat shores, which are hardly suitable for burrows. It is also obvious that the quality of the shore is responsible for the paucity of muskrats in many dystrophic inland watercourses and also in certain areas of the sea coast (p. 42).

When the enthusiasm for muskrats was at its peak in Finland, great hopes were fixed on the idea that the numerous marshes would become a true »muskrat Eldorado» (e.g. Korvenkontio 1925: 32, 134—135). But these hopes were dashed.

On quaking bogs and on peat mosses adequate food is, no doubt, available (*Equisetum, Scirpus, Phragmites, Glyceria, Carex, Menyanthes, Nuphar, Nymphaea,* etc.). Their shallowness and the fact that they freeze deep rule out the majority of them as habitats for muskrats. The absence of muskrats even from deep quaking bog-like and peaty ponds indicates that in such cases the nature of the shore is the decisive factor. The quaking peat shores of bog ponds are not suitable for burrows, although peat soil, as such, is not unsuitable for burrowing in. In connection with the draining of swamps, new habitats have been found for muskrats which they have readily adopted In the North American literature. the author has not found any reports on the occurrence of muskrats in peat-bogs

The scarcity of the muskrat populations in oligotrophic lakes (Table 3) depends not only on the low productivity of the vegetation, but also on the structure of the shores, which are hard and unsuitable for digging (sandy, gravelly, rocky or stony).

In ditches made for the purpose of drainage, muskrats settle down very readily. In Pohjanmaa muskrats have rapidly occupied such biotopes. Trenches dug in connection with the drainage of bogs have likewise been occupied by muskrats, which can easily burrow in their banks. Such cases are known from the Pelso and Konnunsuo bogs where good muskrat catches are made yearly. As soon as the ditch between Lehijärvi and Vanajavesi was completed muskrats took

possession of it at once. (Oral information of the farmer, J. Savolainen.) The North-American muskrat marshes are improved by ditching, which leads to a remarkable increase in the numbers of muskrats. Unproductive marsh areas have thus been converted into very productive muskrat areas (e.g. Arthur 1928, Hamerstrom & Blake 1939, Stearns, MacCreary & Daigh 1940, Hewitt 1942, Lay & O'Neil 1942, Yeager 1943, Lay 1945, Anderson 1948, Errington 1948, Gashwiler 1948, Mathiak 1952). In addition to the stabilizing of the water-level and the improved plant productivity (e.g. Anderson 1948) the better possibilities for digging have also been important in producing this result.

d. Currents

Rivers form the second main biotope of muskrats. Enders (1932: 21) writes: »The habitats of the muskrat in Ohio may be divided roughly in two types: marsh or swamp habitats and stream habitats. There is no accurate method available which would permit an estimate of the relative number of animals in each habitat, but it is the opinion of the writer that the numbers in Ohio are approximately equal. The concentration in marshes is more noticeable but the larger area of stream banks, as compared with marshes, equalizes the numbers.»

The situation is similar in Finland, too. The abundance of vegetation and the nature of the shore affect the muskrats in rivers in the same way as in lakes. In Lapland the muskrats live almost solely in rivers. The lakes there (at least most of them) are much too barren to provide a suitable habitat. In other parts of the country the densities of the muskrat populations are almost equal in river and lake districts (Artimo 1949, Map 10). As the current hinders the very deep freezing of the water and keeps it open even when the lakes are frozen, the unfavourable season for feeding becomes shorter than in lakes and ponds. The author has also observed that in the Kokemäenjoki drainage basin the muskrats in certain lakes (in Suodenniemi: Kirkkojärvi, Koivuniemenjärvi) move to the mouths of rivers, where the water remains open for longer.

e. Other factors

In their native country muskrats have been observed to do best in rather small lakes and ponds (e.g. Merriam 1884, Johnson 1925, Gashwiler 1948). The same is true in Finland (see above p. 49). Here exposure and erosion (wind, swell, erosion caused by ice) can do less damage to the aquatic vegetation (Vaarama 1938: 232). Maristo (1941: 253—262) reports that the effect of these factors upon the aquatic vegetation is directly correlated with the area of open

lake water (i.e. without islands). In the medium-sized and large lakes the aquatic vegetation is always best developed in sheltered bays. The occurrence of muskrats is often restricted to these localities, which represent only a small proportion of the lakes in question (p. 33). In such localities their houses among the vegetation are less susceptible to the destructive effects of wind and swell.

It has not been verified that the salt content of the water has any direct effect on the occurrence of muskrats. Although the main ranges of most muskrat races are situated in regions of inland watercourses, certain races are adapted to brackish waters on the coasts of oceans (*O.z. rivalicius*, Arthur 1928, Lay & O'Neil 1942, Lay 1945 a; *O.z. macrodon*, Smith 1938, Dozier 1947; *O. z. osoyoosensis*, Dalquest 1948). The nominate race thrives in brackish waters, too. Thus McNamara (1949) states that in New Jersey muskrats live on tidal marshes situated 2—4 feet above sea-level and that muskrat trapping is very important source of livelihood there. It has been established, however, that a high salt content is deleterious to muskrats because of its adverse effect on the food plants (Lay 1945 a, Lay & O'Neil 1942, Dozier 1947). In Finland muskrats are common all round the coasts, including the Ahvenanmaa Islands, where the salt content of Finnish waters is highest (about 6 $^{0}/_{00}$).

According to Dailey (1927), industrial pollution can be injurious to muskrats. Hoffmann (1958: 66—67) has reported some cases of death possibly attributable to acute poisoning, but he does not present any direct evidence of the damaging effect of industrial waste waters on muskrat stocks. Dalquest (1948: 361), on the other hand, stated that muskrats can live even in waters polluted by garbage and sewage. Many of the watercourses of Finland are polluted by industrial effluents, chiefly from the wood-pulping industry. A characteristic of the regions near sulphite cellulose factories, however, is the abundance of the higher aquatic vegetation (particularly *Nymphaea* and *Nuphar* associations; e.g. Halme 1950). Such luxuriant *Nymphaea* associations as are found below the Mänttä factory are not seen elsewhere in Finland (Järnefelt 1953). The author has observed an abundant muskrat population in the place in question. According to the local gamekeeper, catches have been good although the water is very polluted and bad-smelling. The author has not heard any complaints that the waste waters of factories have proved harmful to muskrat stocks in Finland.

2. Food

a. Vegetable food

Muskrats are generally regarded as herbivores which, like other rodents, sometimes consume a good deal of animal food.

Widely different marsh and aquatic plants are eaten by muskrats. Almost anything of vegetable nature is tolerated, it is said. This is particularly true during winter and early spring, the most unfavourable seasons in regard to feeding, before the new aquatic vegetation has sprouted.

The list of known food plants of the nominate race comprises about 60 species (Johnson 1925, Enders 1932, Hamerstrom & Blake 1939, Butler 1940, Errington 1941, Hewitt 1942, Takos 1947, Bellrose 1950, Bednarik 1956) but only about 30 of them have any real significance as regular components of the diet. In addition, plant species which are not ordinary aquatic plants (*sensu* Fasset 1940), such as cereals, root and fruit crop plants and ornamental plants and the buds and bark of certain trees and shrubs, are included in the list of their food plants. It has been demonstrated, however, that in spite of a certain variety in their diet, muskrats display preferences, varying both individually, locally and seasonally, for certain food plants. The nature of the food chosen may also change with age.

Very few investigations have been carried out in Finland on the food eaten by muskrats. Korvenkontio (1930) lists 44 aquatic plant species which they do or may utilize as food in our watercourses. The following are, according to him, preferred: *Equisetum limosum, Phragmites communis, Scirpus lacustris, Typha* spp. *Carex acuta, Nymphaea* and *Nuphar*. Further important species are: *Sparganium erectum Stratiotes aloides, Elodea canadensis, Scolochloa festucacea, Glyceria maxima, Scirpus silvaticus, Carex aquatilis, Acorus calamus* (cf. also Valtonen 1959), *Juncus* spp., *Iris pseudacorus* (?), *Polygonum amphibium, Menyanthes trifoliata, Hippuris vulgaris* (?).

Brander (1949, 1951 a, 1951 b) lists the following as the most important food plants: *Equisetum, Scirpus, Phragmites,* and *Carex* species. The following genera are of significance, although they are not the main food plants: *Iris, Nymphaea, Nuphar, Typha, Sparganium, Potamogeton, Polygonum, Menyanthes, Zizania, Glyceria* and the bark of willows (*Salix* spp.) and aspen (*Populus*). Some other plants of rather small size are also mentioned: *Hydrocharis, Sparganium minimum, Utricularia vulgaris, Lemna minor.* Many observers (e.g. Hakola 1926, Harju 1946, Artimo 1949) mention that muskrats also eat cereals and root crops, as they do in their native country.

The plant species eaten by muskrats can be studied by examining the food remains on the feeding platforms (in winter: in feeding huts and in houses). Muskrats are generally very wasteful in their feeding and eat only the succulent basal parts of aquatic plants. The winter food comprises roots and rootstocks of such plants. The plant remains on feeding platforms are easily identified. A heavy swell or rise in water level sometimes scatters the remains in the surroundings, or they may dry up and so become unidentifiable. Usually, however, the analyses of feeding platforms give a reliable picture of the food of muskrats (c.f. e.g. Hamerstrom & Blake 1939, Takos 1947, Bellrose 1950). Data on the quality of food can also be obtained from stomach and faecal analyses (Bednarik 1956, Arata 1959), but their examination is very troublesome and time-consuming (e.g. Errington 1941).

During the years 1945—53 the author analyzed 314 feeding places from different watercourses (Artimo 1957). The majority of them were situated in the region of the Kokemäenjoki drainage basin or elsewhere in the southern part of Finland. Nine analyses were made in the Kuopio district and 5 in Lappeenranta area. The author did not have an opportunity to analyze any feeding platforms in North Finland, in Pohjanmaa or on the coast. 219 of the analyses are from eutrophic lakes, 90 from dystrophic and 5 from oligotrophic lakes. In the oligotrophic lakes muskrats do not generally remain stationary (p. 45) and their feeding places are found there only occasionally and generally in autumn during their most active period. The analyses were distributed according to season in the following manner: 7 in January, 19 in March, 10 in April, 9 in June, 66 in July, 103 in August, 80 in September, 12 in October and 8 in November. In winter the analyses were made from the opened winter houses, but it was necessary to restrict their number to as small an amount as possible. The number of analyses taken in spring, during and after the break-up of the ice is small because at this period hardly any feeding platforms are to be found. The flood water in spring evidently destroys them or submerges them.

Remains of 30 plant species were found on the feeding platforms. There were remains of one plant species on 43 % of feeding platforms investigated, of two on 39 %, of three on 5 %, of four on 3 %, and of more than 4 aquatic plant species on 10 %.

It thus seems evident that the muskrats in Finnish watercourses mainly subsist on a small number of plant species. Takos (1947) reported the following data based on similar analyses made in Maine, U.S.A.: in 50 % of feeding platforms there were remains of only one plant species, in about 25 % of two and in about 25 % of three or more plant species. Moreover, in Ohio, Bednarik (1956) has established that in the course of a year *Typha* and *Sparganium* were the most important components in faecal analyses, so that there were 42 % of the former plant and 37 % of the latter in the samples investigated. Together these two plants accounted for 79 % of the food consumed.

The result of the author's analyses of feeding platforms are presented in Table 4.

In columns 3—7 are presented the results of analyses of 104 feeding platforms from 15 lakes in the Kokemäenjoki basin where the aquatic vegetation has been studied in detail. Of these lakes the following are eutrophic or dys-eutrophic: Kirkkojärvi, Kyläjärvi, Säkkölänjärvi, Suoramaanjärvi, Taivallampi, Ahulinjärvi (all in Kangasala), Mäyhäjärvi and Savijärvi (both in Lempäälä), Kirkkojärvi (in Parkano; all studied by Dr. U. Perttula; archives of the Botanical Institute, Helsinki University). The following dystrophic lakes were also taken into consideration: Poikkeusjärvi and Kairojärvi (in Parkano, both studied by Dr. U. Perttula), Hautajärvi, Kaitalampi, Särkijärvi and Saarijärvi (in Lammi, all four studied by the author). The frequency values represent a modification of Norrlin's (1871) scale, with

Table 4. Food plants of muskrats and their preferences, based on an analysis of feeding platforms. - 1—2: Numbers and percentages indicating the frequency of each plant species on the 314 feeding platforms investigated. 3: Squares of the mean frequencies of the plant species in 15 lakes, where the aquatic vegetation has been described. 4—5: Numbers and percentages indicating the frequencies of each plant species on 104 feeding platforms on these lakes. 6: The area covered (column 3) as a percentage of the total area of aquatic vegetation (140 ha.). 7: The preference for the species (= the ratio of the values in columns 5 and 6). For further details, see p. 54, 56.

	1	2	3	4	5	6	7
A. Reed-swamp species and plants with partly emerged shoots							
1. *Equisetum limosum*	78	24.8	34.8	28	26.9	24.9	1.1
2. *Typha* spp.	23	7.3	2.4	9	8.7	1.9	4.6
3. *Scirpus laqustris*	49	15.6	11.6	15	14.4	8.3	1.8
4. *Eleocharis palustris*	2	0.6	7.3	1	1.0	5.2	0.2
5. *Phragmites communis*	31	9.9	29.2	12	11.5	20.9	0.6
6. *Glyceria maxima*	4	1.3	—	—	—	—	—
7. *Gl. fluitans*	1	0.3	1.0	—	—	0.7	—
8. *Carex* spp.	139	44.3	38.4	51	49.0	27.4	1.8
9. *Sparganium erectum*	14	4.4	1.2	4	3.8	0.9	4.2
10. *Sp. simplex*	13	4.1	9.6	5	4.8	6.9	0.7
11. *Sp. minimum*	—	—	3.6	—	—	2.6	—
12. *Alisma plantago-aquatica*	—	—	7.8	—	—	5.6	—
13. *Sagittaria sagittifolia*	3	1.0	0.5	—	—	0.4	—
14. *Butomus umbellatus*	4	0.3	1.0	—	—	0.7	—
15. *Acorus calamus*	1	0.3	—	—	—	—	—
16. *Iris pseudacorus*	1	0.3	2.0	—	—	1.4	—
17. *Ranunculus lingua*	—	—	0.5	—	—	0.4	—
18. *Hippuris vulgaris*	1	0.3	1.7	—	—	1.2	—
19. *Lysimachia thyrsiflora*	—	—	13.7	—	—	9.8	—
20. *Menyanthes trifoliata*	5	1.6	13.7	4	3.8	9.8	0.4
21. *Calla palustris*	3	1.0	16.8	1	1.0	12.0	0.1
B. Plants with floating leaves a. rooted							
22. *Sparganium Friesii*	2	0.6	8.4	1	1.0	6.0	0.2
23. *Potamogeton natans*	15	4.7	21.2	3	2.9	15.1	0.2
24. *P. gramineus* (*alpinus*)	—	—	3.6	—	—	2.6	—
25. *Polygonum amphibium*	2	0.6	1.2	—	—	0.9	—
26. *Nuphar* spp.	22	7.0	32.5	8	7.7	23.2	0.3
27. *Nymphaea* spp.	7	2.2	6.3	2	1.9	4.5	0.4
28. *Callitriche* spp.	—	—	2.9	—	—	2.1	—
b. free - floating							
29. *Hydrocharis morsus-ranae*	—	—	5.8	—	—	4.1	—
30. *Lemna* spp.	—	—	10.9	—	—	7.8	—
31. *Spirodela* spp.	—	—	2.3	—	—	1.6	—
C. Wholly submerged plants a. rooted or fixed							
32. *Isoëtes* spp.	7	2.2	2.6	2	2.0	1.9	1.0
33. *Elodea canadensis*	1	0.3	0.6	—	—	0.4	—
34. *Potamogeton praelongus*	—	—	0.2	—	—	0.1	—
35. *P. perfoliatus*	1	0.3	3.2	—	—	2.3	—
36. *P. pusillus*	—	—	0.1	—	—	0.1	—
37. *P. obtusifolius*	4	1.3	6.3	1	1.0	4.5	0.2
38. *Scirpus acicularis*	—	—	0.8	—	—	0.6	—
39. *Ranunculus reptans*	—	—	0.4	—	—	0.3	—
40. *Subularia aquatica*	—	—	0.3	—	—	0.2	—
41. *Myriophyllum* spp.	2	0.6	2.9	—	—	2.1	—
42. *Lobelia dortmanna*	—	—	0.3	—	—	0.2	—
b. free-floating							
43. *Stratiotes aloides*	—	—	1.0	—	—	0.7	—
44. *Ceratophyllum demersum*	—	—	1.7	—	—	1.2	—
45. *Utricularia* spp.	—	—	9.6	—	—	6.9	—

fqq = 7, fg = 6, st fq = 5, p = 4, st r = 3, r = 2, rr = 1. Following Ulvinen (1937: 40 ff), the author has taken the squares of these values to represent the areas covered by the different species. In this way it was possible to estimate in percentages (column 6) the proportion of the aquatic vegetation (covering 140 ha.) represented by each plant species. Since the relative amounts of aquatic plant species on the feeding platforms investigated is known (column 5), it is then possible to obtain some idea of what food plant species the muskrat has used most in relation to the amount available, and hence to arrive at the food preference (column 7, forage ratio, Takos 1947). This calculation, of course, gives only a rough picture of the muskrat's order of preference for food plants.

From Table 4 we see that the commonest food plants were *Carex* spp., (in 44, and 49 % of the feeding platforms investigated), *Equisetum limosum* (25 and 27 %) and *Scirpus lacustris* (16 and 14 %). *Phragmites communis*, *Sparganium erectum*, and *S. simplex*, *Typha latifolia*, *Potamogeton natans* and *Nuphar* spp. were also fairly frequently utilized (3—12 %). The other plant species presented have obviously formed a more or less occasional feature of the diet. Korvenkontio (1930) and Brander (1949, 1951 b; cf. also Artimo 1949, 1956, 1957) agree in regarding the same plant species as the most important and commonest food plants.

In previous reports from Finland, *Isoëtes* has not been listed among the food-plant species of the muskrat, but the author found it on 7 feeding platforms. *Isoëtes* may be more important, however, than the value in the table shows, since especially in spring and autumn the remains of *Isoëtes* are found floating in great rafts on the shores of certain lakes. Floods have obviously scattered them from the feeding platforms of muskrats or these animals have loosened the plants from the bottom in eating their basal parts. From the Kola Peninsula Novikov (1936 b) reports that *Isoëtes* is eaten by muskrats. Hoffmann (1958: 39) has confirmed this in Central Europe. No remains of *Stratiotes aloides* were found by the author in the feeding places, although Korvenkontio (1930) mentions that it is eaten by muskrats (in feeding experiments?). Yet in the lakes of the area studied (Kangasala: Kirkkojärvi, Suoramaanjärvi, Säkkölanjärvi, Nuorronjärvi, Taivallampi) this species was fairly common. *Potamogeton natans* and to a lesser degree other *Potamogeton* species also seem to form part of the diet of muskrats and may not be merely emergency food as Korvenkontio (op.cit.) believed. *Potamogeton* was found to have been eaten in lakes (e.g. Taivallampi) where ample supplies of other nourishment were available.

Hydrocharis morsus-ranae and *Utricularia vulgaris*, which are mentioned by Brander (1951 a) as food of muskrats, have not been found to have been eaten in nature (nor any other free-floating plants). In feeding experiments, however, the animals ate this plant (Artimo 1957). Korvenkontio (1930) alleged that *Calla palustris* was not eaten by muskrats, although they might damage this plant by their digging. Marvin (1939) likewise reported that this species was not eaten in experiments carried out in East Karelia. But the present author has observed that small amounts are eaten both in nature and in feeding experiments.

From Table 4 it can be seen that there was a distinct order of preference for the food plants. The highest value (4.6) was scored by *Typha*, sp., which in the American literature is likewise always mentioned as the chief food plant of muskrats. The amount of carbohydrates stored in the rootstocks of this species is 53.4 % of the dry matter (42.8 % starch, 9.6 % proteins; Korvenkontio 1930). Second place was taken by *Sparganium erectum* (4.2) which is also known elsewhere as a good food plant. Then followed *Scirpus lacustris* (1.8), *Carex* spp. (1.8), *Equisetum limosum* (1.1) and *Isoëtes* (1.0), whereas the significance of other species

was small. It will be noted that *Phragmites*, which is very common in the muskrat localities, gets a much lower score. Of the helophytes, muskrats eat *Sparganium simplex* and *Menyanthes trifoliata* to a small extent. Several plants with floating leaves were eaten in small amounts; of wholly submerged plants there was a slight preference for *Potamogeton obtusifolius* only, and *Isoëtes* came next in order after *Equisetum*.

In spite of the rough method of calculation it can be seen that the plant species eaten and preferred by muskrats are helophytes and hydrophytes especially of the tall reedswamp type and rooted plants with floating leaves, whereas the significance of plants belonging to other life-form groups is in both cases small (*Isoëtes* cf. above).

The following list of the plants commonly eaten by the nominate race of muskrat in North America and more or less regularly in Finland shows that 22 (64 %) of the genera are common to both countries. These are marked with an asterisk (+).

+ *Equisetum*
+ *Typha*
+ *Sparganium*
+ *Potamogeton*
Najas
+ *Sagittaria*
+ *Alisma*
+ *Elodea*
+ *Zizania*
+ *Glyceria*
+ *Phragmites*
Calamagrostis
Cyperus
Dulichium
+ *Eleocharis* (*Scirpus*)
+ *Scirpus*
+ *Carex*
+ *Acorus*
+ *Lemna*
Wolffia
+ *Myriophyllum*
Pontederia
+ *Juncus*
+ *Iris*
+ *Salix*
Rumex
+ *Polygonum*
Ceratophyllum
+ *Nymphaea*
+ *Nuphar*
Ranunculus
Sium
Lysimachia
Lycopus

The role of common plant genera would certainly be still greater if more analyses had been made in different parts of Finland. Of the 34 plant genera listed, 31 occur in both areas. Only *Cyperus*, *Dulichium*, *Pontederia* and *Wolffia* do not belong to the flora of Finland.

The Finnish list of food plants adds only three genera, *Isoëtes*, *Hippuris* and *Hydrocharis*, to those recorded as food of North American muskrats. *Hydrocharis*, however, is not a member of the North American flora.

The great similarity of the food plants of American and Finnish muskrats appears convincingly from the list below, where the frequency of plant remains on feeding platforms in Maine (according to Takos, 1947) and Finland (Table 4) are presented. A (+) instead of a numerical value indicates that the species is mentioned in the literature.

Maine	%	Finland	%
Typha latifolia	45	*T. latifolia & angustifolia*	7.3
Acorus calamus (var. *americanus*)	42	*A. calamus*	0.3
Sagittaria »sagittifolia» + cuneata	21	*Sagittaria* spp.	1.0
Carex lacustris	11	*Carex* spp.	44.3
Zizania aquatica	9	*Zizania aquatica*	+
Equisetum fluviatile	6	*Equisetum fluviatile*	24.8
Alisma »plantago-aquatica»	4	*Alisma plantago-aquatica*	+
Ranunculus flabellaris	4	*Ranunculus* spp.	?
Lysimachia thyrsiflora	3	*Lysimachia thyrsiflora*	?
Sparganium angustifolium	2	*Sparganium angustif. (affine)*	?
Sium suave	2	*Sium latifolium*	?
Potamogeton pusillus	1	*Potamogeton pusillus*	?
Dulichium arundinaceum	1	—	
Potamogeton gramineus	1	*Potamogeton gramineus*	?
P. natans	1	*Potamogeton natans*	4.7
Salix discolor	1	*Salix* spp.	+
Phalaris arundinacea	tr.	*Phalaris arundinacea*	?
Eleocharis sp.	tr.	*Eleocharis palustris*	0.6
Nuphar variegatum	tr.	*Nuphar luteum*	7.0
Calamagrostis canadensis	tr.	*Calamagrostis purpurea*	?
Glyceria canadensis	tr.	*Glyceria maxima*	1.3
Myriophyllum sp.	tr.	*Myriophyllum sp.*	0.6
Pontederia cordata	tr.	—	
Glyceria sp.	tr.	*Glyceria fluitans*	0.3
Iris versicolor	tr.	*Iris pseudacorus*	0.3
Leersia virginica	tr.	*Leersia oryzoides*	+
Lysimachia terrestris	tr.	*Lysimachia vulgaris*	?
Potamogeton sp.	tr.	*Potamogeton* sp.	+
Scirpus (Trichophorum) cyperinus	tr.	*Scirpus lacustris*	15.6
Taraxacum sp.	tr.	*Taraxacum* sp.	?
Vallisneria americana	tr.	—	

The great differences in the percentages are probably due to differences between the vegetation of the lakes of the two areas. The list indicates, however, that the muskrats in the two areas do to a large extent utilize the same or corresponding plant species. The same remarkable uniformity also appears when food plant investigations carried out by Hamerstrom & Blake (1939) in Central Wisconsin are compared with Finnish ones. Of the 39 genera, 33 (85 %) were common to both areas.

Owing to similar climatic conditions and geological development there is a remarkable degree of similarity in the aquatic vegetation available to muskrats in Finland and in their native country. The vegetable food utilized by muskrats in the two areas is surprisingly similar. One of the reasons for the success of the introductions of muskrats into Finland is the fact that they came to an environment where it was easy to find food of approximately the same nature as in the original area.

b. Animal food

Crayfish and mussels (especially *Anodonta* and *Unio*) form the main animal food of muskrats in North America. In addition, muskrats have been known to devour insects, snails, fish, aquatic birds or their fledglings, and sometimes frogs, certain reptiles, etc. (Merriam 1884: 275, Hollister 1911, Johnson 1925, Lantz 1926, Enders 1932, Smith 1938, Hamilton 1939, Burt 1948, Dalquest 1948: 361, Rustad 1952, Bednarik 1956, Sather 1958, etc.). Errington (1937 d, 1939 a, 1941) published very detailed notes concerning the animal food of muskrats and pointed out that certain populations are so herbivorus that it is difficult to find any evidence that they utilize animal food at all, whilst in other populations the diet does not differ very much from that of the mink.

It is said that muskrats resort more to animal food early in spring when the aquatic vegetation has not yet developed, and in late autumn and winter (cf. Errington 1941, Stearns & Godwin 1941, Sather 1958). Bellerose (1950: 305), howeved, writes: »In the feeding houses there was little to indicate that muskrats fed upon much animal material during the winter months.» Bednarik (1956) mentions that in winter fish scales and remains of crayfish were found in 47 out of 204 stomachs. In the area which he studied plenty of dead (asphyxiated?) fish were available. In Ohio it was established that during the shooting season muskrats fed on birds that had died of wounds or been shot but not retrieved (cf. also Errington 1941).

Many observations made in Finland indicate that muskrats have retained their fondness for crayfish and mussels, especially (e.g. Korvenkontio 1925, 1926, 1929 a, Hakola 1927, Häppölä 1928, Saravuori 1933, Brofeldt 1934, Artimo 1949, 1952, 1957, Brander 1949, 1951 a, b, c, 1956). Remains of mussels and other gastropods were found on 16 % of the feeding platforms studied by the present author. This is illustrated by the following table.

	Feeding platforms investigated No.	Remains of molluscs on feeding platforms No.	%
January	7	3	43
March	19	14	74
April	10	5	50
June	9	0	0
July	66	9	14
August	103	7	7
September	80	10	13
October	12	2	17
November	8	0	0
	314	50	16

The numerous heaps of mussel shells found on shores were not considered, unless they were accompanied by signs of quite fresh feeding of muskrats.

Most observations concerning mussel eating were made in midwinter and early spring. These observations support corresponding observations made earlier in Finland (e.g. Korvenkontio 1929 a, Brander 1955 a, b,) in Central Europe (Hoffmann 1958:33) and in North America (see above). It seems not unnatural that during the season when the supply of vegetable food is at a minimum the muskrats should use proportionally more animal food than at other seasons.

Brander (1955 b) also suggests that muskrats are likely to use mussels as food particularly in watercourses poor in vegetation, but the present author has also found very large heaps of mussel shells in eutrophic lakes rich in vegetation (e.g. Lake Klappträsk, Espoo).

In the present study, remains of crayfish were not found on the feeding platforms of muskrats but in four different localities in Lake Linnanjärvi, Kangasala, it was observed that muskrats had obviously eaten them (Artimo 1949).

In addition to crayfish and mussels, there are some reliable reports from Finland on the utilization of fish as food, although this feature of the diet has generally been exaggerated (Artimo 1949, 1957 cf. also Hoffmann 1958: 38 and Lavrov 1933). In the stomach contents of 264 muskrats investigated by the author there were no signs of such food or of any other animal food either (cf. also Hoffmann 1958: 33—35). In feeding experiments (Artimo 1957), on the other hand, it was shown that muskrats would eat fishes.

No reliable observations have been made in this country of muskrats eating birds or fledglings or frogs, nor have they been observed to feed on the cadavers of wild ducks during the hunting season (Brander 1951 b). A report of the eating of young ducks may be an isolated event (Artimo 1957).

In the American literature there are no reports of muskrats eating other mammals. In Finland, Räsänen (1930 a, b) observed skins of water voles and other remains in muskrat houses, indicating that muskrats had eaten water voles. In this locality the aquatic vegetation was rich and there was thus no lack of plant food. According to the description, the remains (gnawed skins) were just like what is found in cases of cannibalism among muskrats.

From the occasional use of mammals as food it is only a step to the cannibalism observed in muskrats in their native country (e.g. Merriam 1884:275, Johnson 1925, Enders 1932, Errington 1937 d, 1939a, 1941, Cahalane 1947:530, Burt 1948:228) and in Europe (Chappelier 1948, Hoffmann 1958:40). In Finland cannibalism has also been observed in muskrats in captivity (Artimo 1957).

The similarity of feeding habits in Finland and in America thus applies to both vegetable and animal food. Mussels form the bulk of the animal nourishment, whilst the other components of the animal food may be less important and generally more or less exceptional.

c. Regional differences in the distribution of food

Maristo (1941) has divided the Finnish lakes into certain types on the basis of their aquatic vegetation. Those types where reedswamp species and helophytes (p. 55, Table 4) predominate are found from the south to the northern border of Simojoki and Kiiminkijoki basin (p. 11, area V, Fig. 2). In these lakes the food situation is good for muskrats, because the reedswamp species are preferred. Further north, a type where reedswamp species are less abundant predominates (the so-called *Elodeid* type). In these lakes, aquatic plants with floating and submerged leaves are the main species. In Kuusamo there is a special type of oligotrophic lake called the *Potamogeton filiformis — Chara* type, and in Fjeld-Lapland another type of oligotrophic lake, called the *Carex* type, both with very sparse aquatic vegetation (Maristo op.cit.). The causes responsible for the barrenness of our northern watercourses and the small number of plant species inhabiting them are the shortness of the growing period (Söyrinki 1939: 35) and the extreme temperature conditions in winter (Maristo 1941: 248). Shallow lakes, and especially shallow shore zones, freeze very deep and it is the reedswamp species that suffer most. The species with floating and submerged leaves are more hardy, for their organs for wintering are deeper »so findet auch das verhältnismässig reichliche Vorkommen der Wasserblattkräuter, auch der eutraphenten Arten, in sämtlichen nördlichen Seetypen dadurch seine Erklärung» (Maristo 1941: 251, cf. also Lohammar 1938: 220—235).

In the usually barren watercourses of the north the chief species available to the muskrat are *Carex, Potamogeton,* and *Sparganium.* It is true that the *Carex* species have proved to be liked by muskrats (p. 55, Table 4) but they are not especially fond of the *Potamogetons* and *Sparganium* (Sp. *friesii* and Sp. *affine*). In view of this, the food of the muskrats can become very monotonous in these water systems. In addition, severe winters may still further increase the uniformity of the already sparse diet.

Locally the food situation of muskrats may be fairly good even in Lapland. In Kittilä there are certain lakes of the so-called *Stratiotes* type (Maristo 1941: 197—205) where the vegetation is luxuriant (Kotilainen 1956, Salonen 1956). In these lakes reedswamp species are sparse, whilst plants with submerged and floating leaves predominate. The commonest species is *Equisetum limosum. Phragmites communis* does not occur in all the lakes, either »denn vielerorts ist der Boden auch beim Ufer viel zu locker, als dass die Art dort Wurzel fassen könnte. Im Frühjahr werden wiederum die Wurzelstöcke auf Weiten Flächen durch die bis auf den Boden hinab reichende Eisdecke aus dem Boden gerissen» (Maristo op.cit., p. 199). The following other species are found in these lakes: *Scirpus palustris, S. lacustris, Sparganium simplex, Lysimachia thyrsiflora* (not observed to be eaten by muskrats in the more southern parts of the country) and *Hippuris vulgaris.* Of the plants with floating leaves, *Sparganium simplex* is found in all lakes; other common species are: *Potamogeton natans, Nyphaea candida, Nuphar luteum* and *N. pumilum.* Of the submerged plants *Stratiotes aloides,* many *Potamogeton* species and *Myriophyllum* may be mentioned.

In this region the muskrats became established immediately when introduced in 1933—34 and survived well as separate colonies in the sites where they had been released (Aakenusjärvi, Sotkajärvi, Munajärvi, Kulkujoki). Another population expanding from the direction of the Ounasjoki outlet reached the area in 1950—51 and as a result these northern colonies were absorbed into a more southerly continuous distributional area (Figs. 12—15, p. 26).

Novikov (1936 b) mentions similar observations from the Kola Peninsula where muskrats also became settled and survived well in watercourses with luxuriant vegetation. Bujakovič (1951) reports similar occurrences of separate colonies in the northern parts of Siberia.

Of the animal food available to muskrats in our northern watercourses it may be mentioned that *Anodonta piscinalis* is occasionally found as far north as Kittilä (Luther 1952). *Margaritana margaritifera*, however, although not very common, is distributed throughout Lapland. According to Brander (1955 a), it is significant as muskrat food in North Finland. The distribution of the *Unio* species is more southern. The same is the case with the crayfish, whose range extends to about lat. 62° N. Introductions of this species have been made into some localities in the regions of Oulu—Iisalmi (Järvi 1911), but farther north the species is lacking.

It can thus be concluded that animal food suitable to muskrats is available in Lapland, too. *Margaritana* may perhaps replace the rare *Anodonta* and the *Unio* species, which do not occur in Lapland.

The absence of muskrats from the north of Lapland is obviously due to the poor plant productivity. This scarcity of food has, without doubt, also been responsible for the slow rate of occupation of the southern parts of Lapland by muskrats.

d. Effect of muskrats on the aquatic vegetation

Many American investigators in the muskrat's native haunts mention that the aquatic vegetation occasionally becomes sparser when the animal is abundant (e.g. Pancoast 1937, Krummes 1940, Dozier 1945, Kellog 1947, Dozier et al. 1948). To the best of the author's knowledge, however, detailed investigations have not been made on the nominate race. Of the damage caused by muskrats which very radically disturbed the muskrat marshes in Louisiana, on the other hand, there is a detailed account (Lynch, O'Neil & Lay 1947).

It is a very common opinion in this country that muskrats, especially during their expansion, did considerable damage to aquatic vegetation.

According to investigations carried out by Brander (1949) in Lake Kivijärvi, Urjala, and especially by the present author in 1947—48 in Lake Sarkkilanjärvi, Ikaalinen, in Lake Lampellonjärvi, Lammi, in Lake Kivijärvi, Kiikka, and in Lake Liekovesi, Tyrvää, the thinning of the vegetation takes place in the following way:

In autumn an area of thinned vegetation surrounds each individual muskrat winter house. This is seen very distinctly, especially in the *Equisetum* beds, where the houses are constructed of horsetail rhizomes which have been rinsed clean. Such a house has generally been built in water about 0.5 m. deep; it may project as much as 1 m. above the water and have a diameter of about 1.0—1.5 m. at water level. Inside the house is a den, the approximate measurements of which are: length 0.4m., width and height 0.2 m. An enormous number of rhizomes are needed for the construction of such a house. During the winter the inhabitants of the house continue to feed in the surroundings. The number of animals per winter house is usually 3—5 (e.g. Koskelo 1932, Aldous 1947, Dozier 1948 b) or even more (6—8 Bailey 1937, 11—16 Bujakovič 1951, 13 Shanks & Arthur 1952). Owing to the difficulty of moving about (ice cover!) the foraging trips extend only to the immediate proximity of the house, which during the course of the winter will be more or less completely devoured. As the winter food consists mainly of the roots and rootstocks of aquatic plants and especially as the buds are very much liked (as can be verified from the food remains in the houses), the signs of this activity are still to be seen at the end of the following summer as a bare patch or as very thin place in the vegetation (cf. Brander 1949: 4—16, Figs. 2—3).

If muskrats are allowed to live and multiply undisturbed in watercouses, the number of winter houses the following autumn increases. If any of the foundations remain from the previous autumn a house may be built on them but the new winter houses (which are now situated at the side of the bare patch) have to have new foundations. For these and for the ordinary houses, which extend above the water level, considerable amounts of roots of aquatic plants are used. During this winter a larger population is thinning the vegetation than in the previous autumn, and in late summer the open area will already have widened substantially and become irregularly polygonal (cf. Brander op. cit. p. 16, Fig. 4). In this manner the thinning of the vegetation continues with ever-increasing rapidity. The originally separate openings caused by different colonies may finally be come united (Brander op. cit. p. 18. Figs. 5—6).

The result of the activity of muskrats is thus the disappearance of the vegetation from watercourses. The first opening around the house may be about 25—100 sq.m. After one or two years it may be as much as 5 times as great (cf. Brander op.cit.). The disappearance of aquatic vegetation is even quicker in *Equisetum* beds, where the materials for the construction of houses are the rhizomes of horsetails. In other associations (*Phragmites, Carex, Scirpus, Typha*) the materials used for building the houses are not so much roots as stems and leaves (cf. Brander 1949, 1951 a, Artimo 1952). The destruction is then not so complete and rapid as in pure *Equisetum* beds.

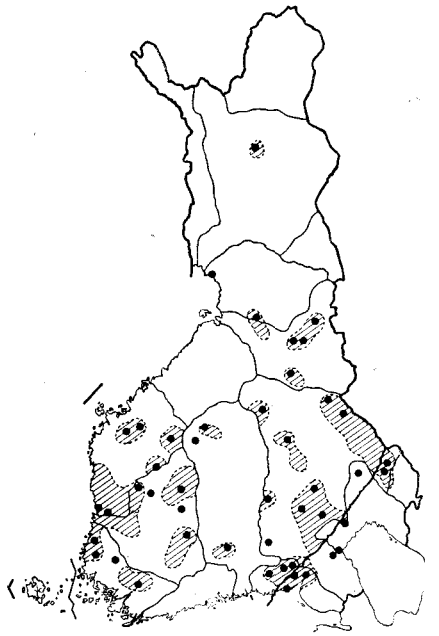

Fig. 19. The introductions of Virginian (blue) muskrats and their distribution up to the end of the year 1945.

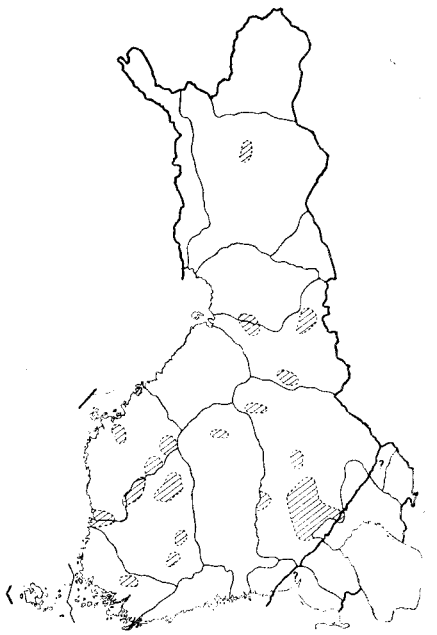

Fig. 20. The distribution of blue muskrats in 1948.

outlet of the Kokemäenjoki drainage area had been reduced to the area of Ahlainen—Noormarkku—Yyteri. The population east of Lake Pielisjärvi had disappeared. Only in the Saimaa district had the area occupied by the blue muskrat remained nearly as large as before.

From many localities of introduction the blue muskrats had totally disappeared or become mixed with the expanding brown populations. Crossing experiments (Smith 1938, Dozier 1948 a) have shown that the dark colour is a recessive character. In the fur trade, it is known that in regions where blue muskrats have been introduced, the quality of the pelt of brown (common) muskrats is better than in areas where the animals are of pure brown muskrat descent (cf. also Voipio 1948, 1950: 119—120).

Data obtained by the Game Research Institute concerning the distribution of blue muskrats in Finland indicate that a further reduction of their range occurred in the years 1950—53 (Fig. 21). In the Saimaa district the distributional area remained almost unchanged, but everywhere else the populations receded or even totally disappeared.

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When the waters are open, muskrats use as their main food the basal parts of the shoots of aquatic plants but will take the roots, too, and it then depends on the size of the population how much their activity affects the vegetation. Autumn and winter, however, are the seasons when, owing to the construction of houses and because of the greater need of food, the destruction of the aquatic vegetation is most intensive.

In watercourses occupied by dense muskrat populations such destruction may reach considerable proportions. In the summer of 1946, there were 75 bank dens in Lake Liekovesi, in Tyrvää. The following winter large numbers of muskrats moved to the lake from the surrounding waters and 250 muskrat houses were built; the year was very dry and the winter food resources everywhere decreased noticeably. But in Liekovesi, a widening of the river Kokemäenjoki, there were as yet no observable changes in this respect. In the following autumn (1947) there were 258 winter houses but in the autumn of 1948 only 150 (Table 1, p. 43). In a few years, however, the abundant muskrat population succeeded in destroying the dense aquatic vegetation of the lake to such an extent that by October 1948 there were great open patches and the entire vegetation was very sparse over an area of about 20 ha. (Artimo 1952, Fig. 12).

The author has no quantitative estimates of the damage inflicted by muskrats on the aquatic vegetation in the entire lakes and watercourses occupied by them, but the following approximate calculations may be mentioned.

In Vähäjärvi in Riihimäki *Equisetum limosum* formed dense and extensive beds before the arrival of the muskrats (about 1932) according to J. Valento (GRI). On July 8, 1947, the author observed that there were only some isolated stalks of horsetails growing on the northern and southern shores. On the western and eastern shores the beds were somewhat larger but very sparse. *Scirpus lacustris* likewise used to form large uninterrupted beds but of these only a few stalks were left. *Typha latifolia* had almost totally disappeared. There were numerous broken passages of muskrat bank leads and den burrows around the lake and some fresh feeding platforms were found. In Paalijärvi, in the immediate vicinity of Lake Vähäjärvi, where muskrats likewise appeared in 1932, there had earlier been a very dense bed of *Nyphaea* and the lake was quite white during their flowering time. On June 8, I counted a total of 10 water-lily blooms. The disappearance of the vegetation from the lake took place mainly in 1936—38 when the muskrat population there was very large. After the destruction of the vegetation the muskrats also disappeared, although some bank dens in the lake have continued to be occupied.

In the period 1935—39, the muskrat stock in Saarijärvi, Lammi, was very large, according to a farmer living on the shore of the lake. Before the arrival of the muskrats *Scirpus lacustris* formed very large beds. In the years 1945—49, 1—2 pairs of muskrats lived in the lake. At the end of this period, *Scirpus* was only found growing sparsely over an area of about 2 sq.m. The horsetail beds likewise disappeared when muskrats occupied the lake in great numbers. *Equisetum* now grows very sparsely around the lake and the water lilies have likewise almost totally disappeared. *Nuphar* has fared better.

According to P. Rajala, M.Sc. (oral statement), by 1946 muskrats in Lake Valkeajärvi in Pihlajavesi had destroyed the *Scirpus lacustris* beds and some of *Equisetum* beds, which looked as if they had been mown. The first muskrats were found in the lake about 1939. Before the arrival of the muskrats the plants had formed a very dense and almost impenetrable reed-swamp.

From Sääminki the fishery adviser A. Mäkelä reports (GRI) that muskrats appeared in Lake Miehikköjärvi in the years 1939—40. In 1943—44 they were very numerous. The shores of the lakes were thickly fringed with rushes but by 1946 these had almost totally disappeared, as had the muskrats too. Muskrats could live in the lake almost undisturbed, for during 5 years at most 30 muskrats were trapped and hence there were no excessive catches to destroy them. In Lake Särkijärvi the number of muskrats was likewise very great. In 1945, a total of 27 muskrats (mainly juvenile specimens) were caught in fish-traps but in the summer of 1946 only one was found dead in a fish-trap. Both the *Equisetum* and *Scirpus* beds and the muskrats had almost completely disappeared.

From Heinävesi the game-keeper E. Hiltunen reports (Nov. 5, 1946) that in the region between Lakes Varisjärvi and Suvasvesi muskrats decimated the *Equisetum* and *Phragmites*. The reed-swamp, which was earlier almost impenetrable by boat, had been remarkably thinned by the dense population of muskrats in 1945—46.

A number of observers of the Game Research Institute, among them Y. Marjamäki from Noormarkku, S. V. Liuksia from Lake Pitkäjärvi in Kokemäki, Y. S. Rissanen from Lake Pielisjärvi, P. Pirskanen from Ruokolahti, and K. Soininen from the Iisalmi district made similar reports.

From the observations reported above, it appears that *Equisetum, Phragmites* and *Scirpus* have borne the brunt of the depredations of muskrats. Damage done by muskrats to *Nymphaea* and *Typha* beds has also been considerable (cf. also Koski 1946).

It is significant, however, that the destruction caused by muskrats has continued only up to a certain point, for when the vegetation grew sparse the muskrats evidently moved away or at least the population became smaller so that there was enough food for the remaining muskrats. For instance in the longest-occupied regions, the area of the Kokemäenjoki basin, there are not, as far as the author is aware, any lakes in which muskrats had totally destroyed the vegetation. Lakes with sparse vegetation occur in many watercourses, it is true, but in most of them it cannot be said that muskrats caused there any large-scale damage. A certain equilibrium is evidently fairly soon reached.

D. Relations with other species

1. Competitors

In Finland only the water vole and the Norway rat are noteworthy competitors of the muskrats in regard to food and habitats.

The water vole (*Arvicola terrestris* L.) is very common in Finland in watercourses fringed with vegetation, i.e. in the type water systems were muskrats thrive. Water voles, however, also live in drier localities, such as gardens, fields, etc. (cf. e.g. Siivonen 1956: 546). At the start of winter water voles migrate from the shores of watercourses to such localities (Werestschagin 1939). Similar observations were also made in Finland (verbal communication from A. Myllymäki, M. Sc.). Thus it does not compete with muskrats during their most critical season.

Like muskrats, water voles subsist on aquatic plants but they generally also feed on plants growing on the shore and on dry land, as is seen from the list of food plants published by Wijngaarden (1954) *inter alia*. According to this author, in the Netherlands at least, the aquatic plants generally eaten by water voles are not identical with those devoured by muskrats. Water voles only eat *Carex* species, *Scirpus* and *Sparganium erectum* to a very small extent, whereas the leaves of *Typha* and *Phragmites* are eaten in large quantities. It must also be borne in mind that during the summer water voles are usually content with the aerial parts of their food-plants (cf. Bergström 1948). They are not such wasteful feeders as muskrats and the shoots left by the latter will still do for water voles, for the author has often observed these animals eating on feeding platforms of muskrats. The author has not observed water voles foraging far from the shore as muskrats do, but it seems that these animals seek their food quite near the shore-line or on dry land.

Morphologically the muskrat is much better adapted for life in water and especially in watercourses which freeze in winter (Werestschagin 1939). In this respect, too, the water vole is more a shore-dwelling animal. In the years 1945—47, both the water vole and muskrat populations were very abundant, e.g. in watercourses in the Kangasala district. Both species could be found towards evening feeding a short distance from one another. It seems clear that the two species can inhabit the same biotopes because their ecological niches are essentially different. A large water vole population has evidently not prevented muskrats from penetrating to new watercourses. On the other hand, muskrats have never been observed to drive away water voles from their habitats, although they have been observed to attack water voles (p. 60).

The Norway rat (*Rattus norvegicus* Berkenh.) occurs throughout South and Central Finland to as far north as Rovaniemi (e.g. Siivonen 1956: 587). It is largely dependent on human settlements. On the shores of watercourses it thrives well during the open water seasons, although its main food is not aquatic plants. Almost nothing is known of its relations with muskrats (cf., however, Bednarik 1956), but at most it can only be regarded as a very local competitor.

Only the water vole has been able to occupy the same habitats as the muskrat, but it has not been able to retard or hinder the spread and establishment of this species in Finland. There is no native species which could sufficiently affect the economy of shore biotopes or utilize the shelter afforded by the aquatic vegetation, the animal food (chiefly mussels) and plant food or the practically unlimited possibilities for the construction of nests. Everywhere in Finland there are lakes and ponds, suitable for muskrats, which are in the process of filling in, and the muskrat has thus been able to fill an »ecological vacuum.» In this process of

establishment and expansion, lack of competition has evidently been one of the most important factors (cf. also Hoffmann 1958: 130).

2. Predators

In addition to man, muskrats have many enemies among the vertebrates which exterminate even considerable muskrat populations.

The main enemy in North America is the mink (*Mustela vison* Schreb.), whose range roughly coincides with that of the muskrat and which has evidently become specialized to prey on muskrats. Porshild (1945), for instance, mentions that in the delta of the MacKenzie river the main food of the mink consists of fish and muskrats. Errington (1939 a, 1943, 1946, 1954 a) reports that every year minks cause severe losses of muskrats. As a result of long-term investigations, however, he has come to the conclusion that the significance of minks in reducing muskrat stocks has been grossly overestimated. The majority of muskrats killed by the mink have been individuals driven away from suitable habitats and the mortality among such specimens is always high. The views presented by Errington deserve special attention here, because the minks that have escaped from farms especially in the coastal areas of Pohjanmaa and S. W. Finland (Siivonen 1956: 289) have increased in numbers to such an extent that they will soon become an important predator of muskrats in Finland, too. In 1952, a mink nest was found in Kauhava in which there were 18 muskrat tails (verbal information from the game warden, V. Huhtala).

Our native mink, the European mink (*Mustela lutreola* L.), is known to prey upon muskrats in the Soviet Union (Lavrov 1931) and in Finland (Siivonen 1956: 280). As European minks occupy the very biotopes which the muskrats have invaded, it might be expected that they would have benefitted from a new quarry and multiplied, so hindering the spread of the muskrats. But at the time of the first introductions of muskrats it happened that the numbers of European minks were beginning to decrease remarkably. In 1938—39 the decrease continued, and in 1940 the situation was frankly alarming: in 97.7 % of the communes in this country it had either totally disappeared or was only occasional, in 2.7 % the decline had ceased but the population was sparse. In only 0.6 % of the communes in Finland was there a sizeable European mink population (Voipio 1946). This low thus coincided with the very period when muskrats were extending their area at a rapid rate, and explains why the European mink did not retard the expansion of muskrats in Finland.

The European polecat (*Mustela putorius* L.) is stated to have eagerly attacked muskrats in Central Europe (Ulbrich 1930, Hoffmann 1958) and in the Soviet

Union (Lavrov 1931). Several similar observations have also been made in Finland (Räsänen 1930 a). During the mild winters of the 1930's the range of this species reached a maximum and it was fairly abundant in Finland (Kalela 1940, 1948). However, although this species often lives beside water in summer, its winter habitats are mostly elsewhere — in the vicinity of human habitations. Being a less specialized species in regard to its feeding habits, the European polecat hardly had any noteworthy effect on the expansion of the muskrat.

The fox (*Vulpes* spp.) is known to be a formidable enemy of muskrats in North America. Many investigations concerning the food of foxes indicate that particularly in autumn, winter and spring it preys on muskrats (e.g. Crosman 1927, Nelson 1933, Errington 1935, Hamilton 1935: 19—20, Hamilton, Mosley & McGregor 1937, Hatfield 1939, Scott 1943). According to Smith (1938), in Maryland »practically all trappers regard foxes as serious pests on marsh» (cf. also Harris 1952). Errington (1937 c) established that in 200 red fox dens in Iowa 1.3 % of the food remains originated from muskrats. In the previous years the figure was slightly lower. Furthermore Errington (1940, 1943) mentioned that the great drought of 1934 increased the proportion of muskrats in the diet of the foxes (cf. also Murie 1936, Errington & Scott 1945). Gashwiler (1948) reports that in winter the foxes in Maine watch practically all muskrat houses and destroy many muskrats caught outside their protecting houses. Similar observations have been reported from the Soviet Union (e.g. Tretpak 1955).

In Finland many observers have reported that muskrats contribute to the diet of foxes (*Vulpes vulpes* L., e.g. Tiitola 1938, Kähkönen 1946, Turunen 1948, Brander 1950 b, 1951 b). Lampio (1949, 1950, 1953) reports that out of 325 fox stomachs analyzed, 3.7 % contained remains of muskrats. The percentage was smallest in summer and increased steadily towards winter and spring. These data indicate that foxes attack muskrats in Finland in about the same degree as in North America. If the analysis had been confined to the stomachs of foxes living near watercourses, the percentage feeding on muskrats would certainly have been higher. It is known that immediately the ice is thick enough to bear them foxes start visiting muskrat houses and try to tear them apart. During the course of a single winter they examine every muskrat house many times (Artimo 1949, 1952, Brander 1951 b). After severe cold when the walls of the muskrat houses have already frozen hard the foxes often fail in their attempts, but after long mild periods and in late winter they have been observed to take muskrats from the houses (e.g. Turunen 1948). Even if the muskrats escape, the destruction of the houses and the plunge holes will make their existence more hazardous at just the most critical period of the year. During very hard winters plunge holes may freeze; then the animals must move to other watercourses and fall an easy prey

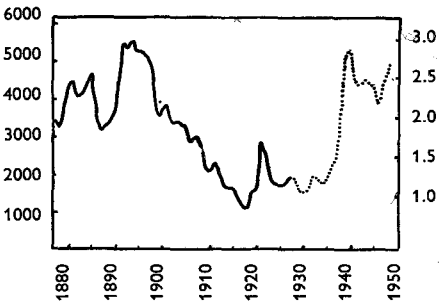

Fig. 36. Fluctuations of the fox population in Finland in the years 1877—1949 according to the shooting statistics (left) and the game inquiries (right) of the Finnish Hunter's Association (Lampio 1951).

to foxes, dogs and other enemies. In this way foxes evidently reduce our muskrat populations considerably.

Remarkable fluctuations have occurred in the fox populations of Finland (Fig. 36). In the 1920's and 1930's when the muskrat was increasing in numbers and extending its range in Finland (Fig. 18, p. 28), the fox population was minimal, but at the end of the 1930's it suddenly increased. In spite of this, the muskrat populations continued to increase. Since the beginning of the 1940's the fox population has remained very large. During the same period the muskrat stock has alternately increased and decreased and the expansion has continued, although at a slower rate. The danger represented by foxes was thus least during the period of the most rapid expansion and increase of the muskrat population in Finland, but foxes have obviously had no essential influence on the recent changes (since the beginning of the 1940's, Fig. 39).

In Canada the caribou (*Rangifer caribou* Gm.) causes great damage to muskrat stocks by eating the houses, especially in years when food is scarce (e.g. Trippensee 1948: 367). In Lapland the reindeer (*Rangifer tarandus* L.) is likewise known to have destroyed muskrat houses (Järvinen 1950: 153—154). V. A. Ruokonen (oral statement) observed that the materials used for construction of winter houses is very sought after as food by reindeers, which destroy the winter houses even more throughly than foxes.

The significance of birds of prey in Lapland in reducing muskrat stocks may be considerable, too. Thus Brander mentions (cf. Hoffmann 1958:64) an observation made by V. Salkio, taxidermist, in Pelkosenniemi according to which remains of 2 muskrats were found in an eagle's nest, but after 2 weeks there were pieces of 30 muskrat specimens.

The fact that, practically speaking, there has been no predatory animal here corresponding to the mink in America may possible have assisted the expansion of muskrats in Finland. There is nothing to indicate that the temporary abundance of foxes had constituted any essential obstacle to this expansion.

IV. REPRODUCTION

A. Changes in nesting habits

During the season of open water muskrats live in bank dens on the shores of watercourses. Such dens consist of a hole situated in a very sheltered place, between tussocks, among aquatic plants, under a stone or protected by tree roots, from which a passage runs into the bank. After 1—10 m., depending on the steepness of the bank, this widens into nesting or dwelling burrows. These generally number 1—3, sometimes more. There is also sometimes more than one passage leading from the water level. A long-used bank den forms an intricate system of passages and burrows and it is there that muskrats give birth to their young during the summer or more seldom in grass dens built near the shore-line among the vegetation (cf. Artimo 1952, 1956). Muskrats may also live in bank dens in winter, particularly in river systems.

The houses are of different sizes and consist of a variety of materials (roots, stems or leaves of aquatic plants, cf. e.g. Brander 1949, 1950 a, 1951 a—c, Artimo 1952, 1956 and above p. 63). They are built in autumn before the freezing of the watercourses and are generally situated near the openings of bank dens, not far from the shore at the outer limit of the vegetation (cf. Koskelo 1932). In extensive reed-swamps (e.g. in bays or in ponds that are filling in) these winter houses may be situated anywhere within the region of the vegetation, even very far from the shore, and then are not all grouped near the openings of bank dens. The houses are used in winter both as dwelling sites (dwelling houses, with bank dens) and as breathing places to make foraging trips under the ice easier (feeding huts or shelters). In running water these winter houses are not built at all, and muskrats live throughout the year in their bank dens.

In the North American literature it is mentioned that the nominate race gives birth to its young both in houses and bank dens. Judging from the descriptions, these constructions are very similar to those observed in Finland (e.g. Johnson 1925, Lantz 1926, Burt 1948, Dozier 1948 b, Bednarik 1956, etc.) In some places such as shallow muskrat marshes, muskrat houses are common, and then there are no bank dens. Hodgson (1924: 11) says: »Some people divide muskrats into two species, thusly — house and bank muskrats. This is erroneous for the simple reason that they build their houses of necessity out of the materials most easily secured and a house muskrat one year, in a certain locality may be a different species the next, because it builds its home in the bank of a stream. ··· Where muskrats live in marshes there are no banks, but there is any amount of bulrushes and other roots and grasses out of which they construct their homes.»

Johnson (1925: 261) likewise reports: »As in the case of beaver, muskrats do not always build houses. Whether they do so or not depends a great deal upon local conditions.» (cf. Dozier 1948 b). Concerning the stream-dwelling muskrats in Iowa, Errington (1937d: 415) states: »A scattering number of lodges or feed-houses constructed of mud, debris, and fresh vegetation may be seen, but these are usually flooded or swept away in due time.» Gashwiler (1948) mentions the two ways of nesting in Maine and Sather (1958) reports the same thing from Nebraska (*O.z. cinnamominus*), while according to Bednarik (1956), muskrats only build houses in Lake Erie in Ohio.

In Finnish watercourses the young are very seldom born in muskrat houses. At the commencement of their spread (in the 1920's and 1930's) muskrats generally gave birth to their young in houses similar to the winter houses. Kivirikko (1940: 83), for instance, writes that on shallow shores the houses are built of aquatic plants about 1 m. above the water level, inside which there is a nest burrow lined with grass, but in steep banks it builds bank dens. Nowadays, however, nesting in houses is a very rare and local phenomenon. The young are almost always born in bank dens. Unfortunately, there were no detailed studies on nesting in houses in the early days, but this may have been a very common phenomenon in watercourses with shallow shores and ample vegetation, as is indicated by the following reports of the observers of the Game Research Institute (1945):

Alavieska, S. Nunala: nests only in bank dens, at one time used sometimes to nest in houses. Alavus, N. Järvilehto: in the past muskrats generally nested in houses, now they have begun to nest in bank dens. Eura, F. Elo: muskrats mainly nest in houses. Eurajoki, G. Merikoski: in houses but also in bank dens. Forssa, H. Lahtinen: nests in houses when undisturbed, but actually mostly in bank dens. Honkalahti, A. J. Antila: muskrats have begun to nest in bank dens because they have been disturbed. Huittinen, H. Kirro: muskrat houses are found in marsh ponds. Ilmajoki, M. Rintala: in some woodland ponds I have found 4—5 muskrat houses, which are inhabited. Generally it nests in bank dens. Joutseno, A. E. Vesomaa: sometimes nests in muskrat houses. Jämsä, H. Huhmarkangas: now nests in bank dens, I have found only 5 muskrat houses. Jämsänkoski, E. Koskinen: there used to be muskrat houses. Nowadays the muskrats nest in bank dens. Karstula, I. Takkula: I have observed soon after their arrival in the locality that muskrats nested in houses, later almost only in bank dens. Kaustinen, V. Valo: muskrat houses have almost totally disappeared, so I think they nest in bank dens, for they still live in the locality. Kiikka, T. Kero: nests in bank dens but young have also been found in muskrat houses. Kinnula, V. Kinnunen: nests in bank dens. I have not seen any houses for some years. Konnevesi, H. Moilanen: nests in bank dens, seldom in houses. Kortesjärvi, A. Karpi: at first they nested in muskrat houses, now mainly in bank dens. Boys destroy muskrat houses in autumn. Koskenpää, E. Blom: muskrat houses are found only on those shores where it is impossible to dig bank dens. Lappajärvi, M. Sadeharju: muskrat houses are found only in remote localities, for men destroy them. Porvoo, F. Wickström: young have been found both in muskrat houses and in bank dens. Raippaluoto, S. Westergård: previously nested in houses, now only in bank dens. Rautalampi, M. Hytönen: nests in houses, very seldom in bank dens. Simpele, R. Vartiainen: muskrats nest in bank dens. I have heard that muskrat houses were found only in Lake Saarijärvi. Taipalsaari, V. Utriainen: in muskrat houses. Tammela, E. Tuomola: at first muskrats nested in houses but once they had settled, they changed to bank dens. Viitasaari, H. Halmesmäki: after its arrival (1930—31) nested for some years in houses, later almost entirely in bank dens. Vimpeli, J. Hakalahti: nests in bank dens.

20 km. from the church muskrat houses are found in ponds. Ähtävä, U. R. Finnäs: nests in bank dens because the houses used to be destroyed.

In addition, the author has observed that muskrat houses still occur in the communes of Eurajoki, Eura and Taipalsaari.

In the summer of 1945 the author made observations on nesting in muskrat houses in many remote woodland lakes with very shallow shores and luxuriant vegetation in Eurajoki and on the border of the communes of Eura and Lappi. In the low banks of these lakes digging would obviously have been very difficult. In three muskrats houses there were young (Melajärvi June 19, Mutajärvi June 19, and Lutanjärvi June 22). In Mustajärvi there were six large houses on June 19, but of these I could examine only one. It was empty but, judging from fresh food remains, it was inhabited.

Another region where muskrats still generally nested in houses in 1947 was Taipalsaari. There in summer (Aug. 6, 1947) I found in Soikkala bay many muskrat houses in use in a luxuriant *Scirpus-Equisetum-Phragmites* reed-swamp. The water had sunk 0.5—1.0 m. In one house there were young. Numerous obviously uninhabited bank dens were observed on the shores. The long trails leading from their openings were visible on the shore, which had become bare. In one case the trail led to an abandoned winter house which was quite high and dry too. Owing to the difficult water situation the muskrats had apparently begun to nest in houses. The observer at Taipalsaari (V. Utriainen) reported that the muskrats there usually nested in houses (see above, cf. also Ojasti 1952). J. Ojasti later reported (oral statement 1956) that muskrat houses were no longer so common as they had been. Muskrats reached Taipalsaari in 1940—43 and in 1947 they were therefore still newcomers.

What, then, has caused the decreased nesting in houses in Finland and the tendency to nest mostly in bank dens?

Some of the muskrats introduced into Finland originated from Central Europe where they nest mainly (river and canal systems) in shore banks (Hoffmann 1958) but muskrats were also imported to Finland from North America, where both modes of nesting occur. Of one batch it was expressely stated (GRI) that the muskrats were not accustomed to dig in banks but nested in muskrat houses. Certain populations may perhaps be specialized to one or other of these modes of nesting, whilst others have variable nesting habits. If specimens belonging to both types were introduced, it is not surprising that both modes of nesting occur in Finland. The fact that muskrats nested in houses during the first phase of establishment seems to be beyond doubt. One of the reasons which have led to the discontinuance of nesting in houses may perhaps be the fact that when the muskrat populations increased, they considerably diminished the reedswamp vegetation, i.e. the material needed for the construction of muskrat houses. The decrease of aquatic vegetation can hardly, however, have been the reason, because the number of winter houses has not decreased but, on the contrary, these have become commoner all over the country. Indeed, the first young in spring were generally born in houses preserved over winter and repaired. It was not even necessary to build new houses for them.

The cause of the change in nesting habits may be the fact that houses were very generally destroyed in the 1920's and 1930's. This destruction was partly due to ignorance but to some extent it was deliberate, because the muskrat was an unwelcome newcomer in fishing waters, where it did much damage to the fishing nets. This damage was generally greatly exaggerated. The significance of the muskrat as a fur-bearer was then not generally recognised. And it was in spring that the houses were most liable to be destroyed when they were unprotected by the vegetation, whereas in autumn and early winter the vegetation, weak ice and snow protected them. Thus the populations which nested in bank dens survived best. According to the observations cited above, muskrats in remote lakes have preserved their habitat of nesting in houses longest, probably because they were undisturbed.

It is a sign of the great adaptability of muskrats that they can give birth to their young either in houses or in bank dens. In each individual case local conditions determine which nesting habit will be used (cf. also Hoffmann 1958: 76). Originally both modes of nesting occurred in Finland, but evidently the destruction of houses by man caused the animals to abandon them as nests, if not entirely, at least to such an extent that it is possible to speak of a change in nesting habits in connection with acclimatization. Muskrats, however, are able to adapt themselves to certain changes in the environment that may occur during the breeding season (e.g. great changes in water level, cf. p. 72) by beginning to breed in houses again.

B. Attainment of sexual maturity

There exist very conflicting data on the age of sexual maturity of muskrats. According to Arthur (1928), in Louisiana these animals reach sexual maturity at the age of 6 months. Lay (1945) states of the same race (*O.z. rivalicius*) that in Texas the first young are born before the mother is one year old, perhaps even at the age of 6 months. LeCompte (1925) and Lantz (1926) report of the muskrats in Maryland (*O.z. macrodon*) that the specimens born in spring breed in the autumn of the same year. Most writers dealing with more northern races, on the contrary, deny that this is possible (Jonson 1925, Errington 1937 b, 1939 b, Highby 1941, Grimm & Roberts 1950, Roslund 1951, Wragg 1953). Even so, however, in certain years specimens are found which have bred within a year of their birth (Errington 1951, 1954 b, cf. also Sather 1958). According to Cahalane (1947: 536) when 9—10 months old muskrats may already give birth to young. Bednarik (1956) confirmed this for muskrats in Ohio marked as juvenile specimens and trapped gravid at this age. Miegel (1953) come to the conclusion that in

Central Europe muskrats have already reached sexual maturity at the age of 5 months (cf. also Hoffmann 1958: 48). From the British Isles Warwick (1940) reports that there is no evidence that muskrats breed before they are one year old.

In Finland, the author has examined altogether 46 juvenile muskrats (21 males and 25 females) caught in the period August—February 1946—47. They were verified to be juvenile or subadult specimens on the basis of the degree of extrusion below the bone line of the anteriormost buccal fluting on the first upper molar (Sather 1954, Olsen 1959a). No signs could be seen in the genital organs that these specimens had bred: their uteri were stringlike and thin, with hard walls. There were no signs of placental scars. The testes of the males were distinctly smaller (cf. Errington 1939 b) than in adult males examined simultaneously.

These observations indicate that in Finland muskrats do not breed during their first year, but by the next spring they are already capable of reproduction, for in male muskrats (70 specimens) caught in and after mid-April descensus had taken place and study of the teeth showed that 58.5 % of them were young of the foregoing summer, the rest older.

C. Number of litters

The gestation period varies from 20 to 30 days (Errington 1937 b, Smith 1938, Enders 1939, Forbes & Enders 1940, Beer 1950, McLeod & Bondar 1952, Wragg 1953, Bednarik 1956). Observations made in nature also indicate that litters are born at intervals of about one month (Errington 1937 b, 1940, Gashwiler 1950, Dorney & Rush 1953, Olsen 1959b). The number of muskrat litters were thus chiefly dependent on the length of time suitable for reproduction. In the region of severe climates they have no time to produce as many litters as in areas with milder climates.

The question of how many litters the *same* female is able to produce during the breeding season is very difficult to determine by observations made in nature. Very rarely is it possible to make observations on the same female during the entire breeding season, but to ascertain the number of litters the counting of placental scars has been recommended. Although there has been no detailed study of their reliability as indicators of the number of young born, results based on their number (McCann 1944, Sooter, 1946, Beer & Truax 1950, Gashwiler 1950, Grimm & Roberts 1950, Roslund 1951, Wragg 1953, Wilson 1955, Sather 1958, Olsen 1959b) are very consistent and thus seem to correspond to reality.

The number of litters of southern muskrat races (*rivalicius, macrodon*), which breed almost the whole year round, varies from 3—6 per year (LeCompte 1925, Lantz 1926, Arthur 1928, Svihla & Svihla 1931, O'Neil 1949, Wilson 1955). Only

2—3 litters, however, have been noted in caged muskrats (Smith 1938, Leonard & Gorman 1946, Harris 1952).

It is considered that 1—2 litters per year is the rule in northern races (e.g. Shiras 1921, Bailey 1929, Porshild 1945, Stevens 1953). From Iowa, Errington (1937 b, 1954 b) gives 2.3—2.9 (2—3) litters per female as an approximate figure for the nominate race. In certain years the number of females which have produced 4 litters may be even as great as 23 %. Wragg's (1953) observations from Ontario based on placental scars and on young in the field indicate that muskrats there produce two litters a year. According to Beer (1950) and Mathiak & Hale (1953), in Wisconsin muskrats have as many as 3 litters in certain years. In the northern parts of the range of the nominate race muskrats thus produce approx. 2—3 litters per year (cf. also Gashwiler 1950, Bednarik 1956).

Corresponding results have been obtained in Central Europe, where muskrats are said to produce 3—5 litters a year (Ulbrich 1930, Mehl 1931, Miegel 1953). According to Pustet (1936), the commonest number is 3. Hoffmann (1958: 48) writes: »Für Sachsen-Anhalt, und damit wohl auch für andere Gebiete Mitteleuropas, können als Norm vier Würfe angenommen werden, nämlich drei von den Alttieren und ausserdem noch ein Wurf von den Jungtieren des 1. Wurfes. » In France muskrats generally produce 3 litters a year (Chappelier 1948). From the British Isles it is mentioned that two litters are common and 3 rather rare (Warwick 1940: 184). In the Soviet Union, Vinogradov & Gromov (1952) have established that muskrats in northern regions have 1—2 and in more southern localities 3—4 litters per year.

There are only a few field observations from Finland. From Kurkijoki Räsänen (1930 a) reported that on Aug. 23, 1930, two juvenile muskrats weighing 190 grams and 470 grams were caught in the same pound trap, and supposed that in the watercourse in question a female specimen had possibly produced two litters during the summer. Korvenkontio (GRI) reported that in September 1928 two litters were found in adjacent passages of a single bank den in Lammi. Each consisted of 5 young, some being large spring young, others small and about the size of water voles. A similar observation was made at the same time on the southern shore of Lake Kuohijärvi (Lammi).

In 1947—48 the Game Research Institute arranged for a trapping party of 16 men to collect material throughout the year to settle the question of the breeding season of the muskrats. In addition to this material, the author had at his disposal more recent material sent to the Game Research Institute. In the records of Korvenkontio (GRI) there are some notes about nests. In the Zoological Museum of the University of Helsinki there are specimens, caught during the period 1929—32, of juvenile muskrats and young taken from nests. On the basis of this material and additional personal observations made in the years 1945—48, it has been possible to compute the time of birth with the aid of measurements published by Errington (1939 b) and Dorney & Rush (1953, cf. also Olsen 1959 b).

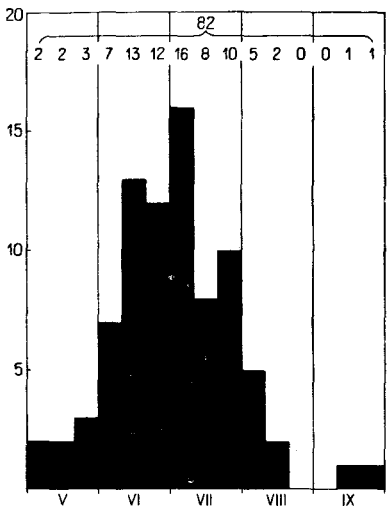

Fig. 37. Dates of birth of muskrat litters.

In Figure 37, data on the date of birth of 82 muskrat litters are presented. It seems that the first young are born in the first week of May. Their number then gradually increases and most young are born in the first week of July. The last are born in mid-August but some even as late as the middle or end of September (one observation of each). In the records of Korvenkontio (GRI) there is a note that in Lammi in South Häme 4 blind young were found at the beginning of September (1929). They were consequently not more than 2 weeks old. The observations from different years thus show that in South and Central Finland the young are born from the beginning of May to mid-August, most of them, however, during June-July. Korvenkontio (1929 a), however, stated, that the late litters are not born until September-October — which has been verified — and that they are still half-grown at New Year. According to Airaksinen (1927), the autumnal young are not yet mature at the beginning of December whilst some are still quite undeveloped. This refers, of course, to observations of rather late litters.

In Soviet Karelia, the breeding season of muskrats begins, according to Marvin (1939), during the break-up of the ice, i.e. just as in Finland. Owing to the more continental climate of Soviet Karelia, the time for the break-up of the ice is somewhat later than in Finland, and breeding thus starts later than in South and Central Finland. The first litters appear there in May-June. The last litter found was born in the second week of September. Such late litters are known in Finland, too, but they are probably not very common in East Karelia either. The earlier onset of autumn in that region may limit the breeding season to a rather shorter time than in South and Central Finland.

Examination of placental scars in 20 muskrats sent to the author in 1947 showed that only 4 of these females had placental scars. The very distinct scars were visible as dark brown, almost circular spots 0.5 cm in diameter. In a specimen caught in Tyrväntö on Sept. 10 there were 11 (5+6) placental scars. This female had thus obviously had two litters. In a female from Lokalahti trapped on Sept. 9 there were only 5 scars (3+2); it had thus produced only one litter. A specimen caught at Ylämaa on Dec. 7 had 12 scars (6+6) and a female trapped at Kangasala on Dec. 21 had 14 (7+7) scars. Both the latter had obviously had two litters.

These observations indicate that, in the southern parts of Finland at least, muskrats produce two litters per summer, but some females only one. The length of the breeding season, from May to mid-August (cf. Fig. 37) and the production of litters in nature at intervals of about one month (p. 74) would make even a third litter possible, but there is so far no evidence that this occurs. Reports that in Finland, too, muskrats produce 3 litters during the summer (e.g. Hannelius 1948) do not appear to be based on field observations.

D. Size of litters

In the southern muskrat races (*macrodon, rivalicius*) with a much longer breeding season (LeCompte 1925, Lantz 1923, Arthur 1928, Svihla & Svihla 1931, Smith 1938, Lay 1945, O'Neil 1949, Harris 1952, Wilson 1955) the approximate numbers of embryos (3.6—4.4) and young born (2.4—3.0) are, in complete accordance with Rensch's rule, distinctly lower than those of the nominate race (6—9 and 3—9, Johnson 1925, Errington 1939 b, 1951, Seemans 1941, Hewitt 1942, McCann 1944, Burt 1948, Mathiak 1948, Beer & Truax 1950, Gashwiler 1950, Grimm & Roberts 1950, Roberts & Early 1952, Dorney & Rush 1953, Wragg 1953, Bednarik 1956). When transferred to more southern localities, the nominate race has maintained its higher number of embryos and young. Although in California, for instance, its period of reproduction is very long, the number of embryos is nevertheless 5—6 (Dixon 1922, Sooter 1946). Correspondingly, the muskrats in Central Europe, where the reproduction period is likewise very long (according to Hoffmann, 1958, December is the only month in which embryos have not been found), have maintained the high number of embryos and young typical of the race. According to Hoffmann (op. cit.), the mean number of embryos is 6.8 and according to Miegel (1953) the number of young varies so that it is approx. 7 in the first litters, later 4—5, but in young muskrats 3—4 (cf. also Warwick 1940, Matthews 1952). The same is true of muskrats of the nominate race acclimatized in the region of Syr Darja, in which the average number of embryos is 8 (Lavrov 1950).

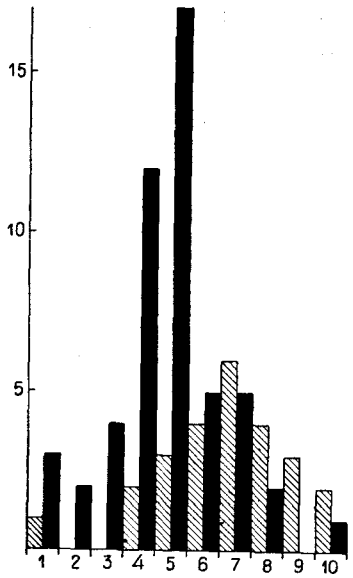

Fig. 38. Numbers of embryos (hatched) and young (black columns).

The data on the numbers of embryos of 25 muskrats caught in South and Central Finland and the number of young in 51 nests found, are presented in Figure 38. The numbers of embryos in Finnish muskrats varies between 1 and 10 (mean 6.8). The mean is thus approximately the same as that of the nominate race in its native country. Raekallio (1938) reported that as many as 12 embryos were found in Finnish muskrats but such numbers may be exceptional.

The number of young in litters varies between 1 and 10 (mean 4.8). The mean corresponds to the lower means reported for the nominate race from the native area. From Soviet Karelia Novikov (1936 a) reported that the numbers of young varied from 4 to 6. As the data available so far are rather meagre, however, it is not yet possible to conclude that in Finland and in Soviet Karelia the mortality of embryos (or young) is higher that in the native area in North America.

V. POPULATION TRENDS

A. Growth of muskrat populations

The changes in muskrat populations can be followed from the annual reports of the observers of the Game Research Institute and the Association of Finnish Hunters (p. 9). From the graph based on these notes (Fig. 39) the following points emerge:

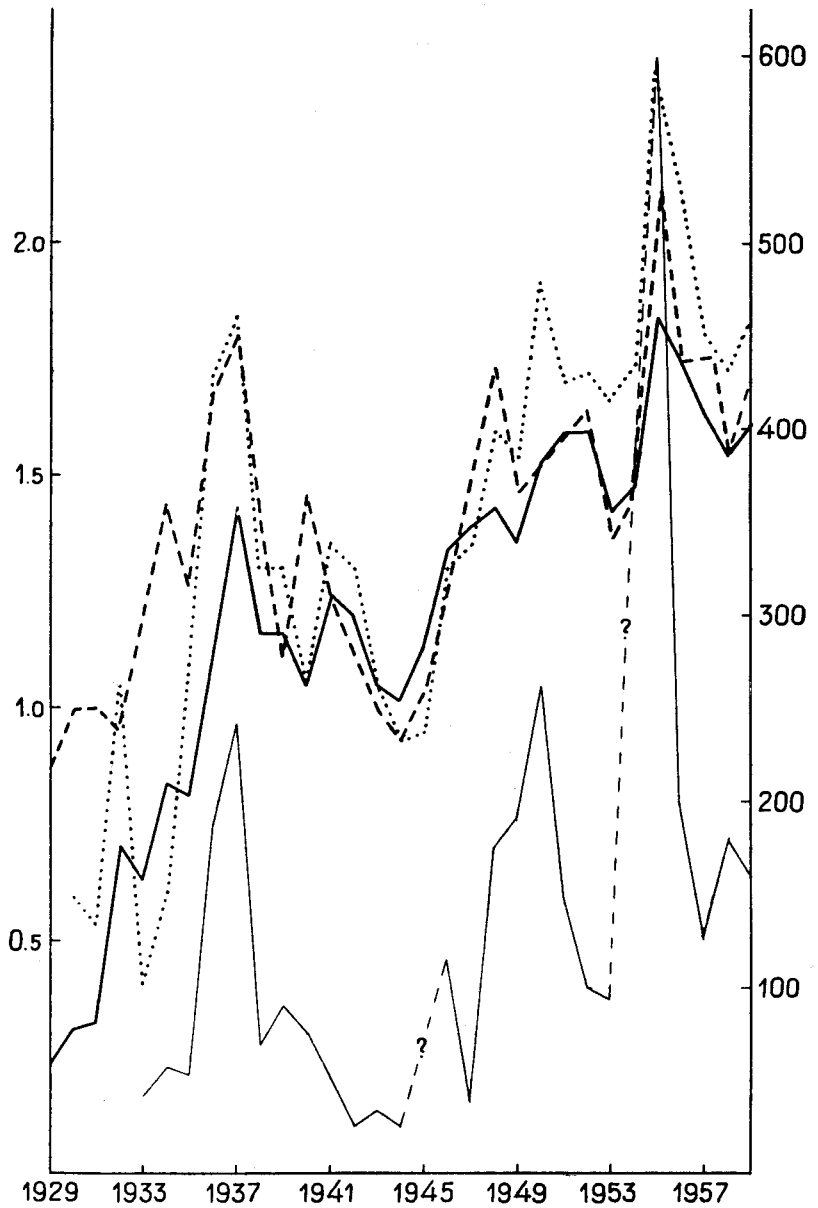

Fig. 39. Fluctuations of muskrat populations (scale at left) and catches (right). Fluctuations of populations (———) and catches (———) in the entire country. Fluctuations of populations in the province of Vaasa (·····) and Häme (— — —).

Muskrat populations in this country increased remarkably between the years 1929 and 1937, when the first great maximum occurred. During this period muskrats colonized extensive regions in South and Central Finland (Figs. 10—12). A distinct and considerable decline took place after the year 1937. Although a slight rise could be observed in 1941 a distinct minimum occurred in 1944. Even after 1937, muskrats continued to invade new areas in South and North Finland (Figs. 13—16). After the minimum of 1944, a new period of increase began. In spite of slight decreases during certain years, the population in the spring of 1950 was already stronger than it had been during the previous maximum (1937). The increase then continued, only interrupted by a slight low in 1953, until the spring of 1955, which was the peak year of the Finnish muskrat populations. In the years 1956—1958, a distinct decline has again been observable.

The fluctuations in numbers of the muskrat populations of the oldest muskrat areas of Finland, i.e. in the provinces of Häme and Vaasa, are very typical of the situation throughout the country (Fig. 39). Muskrats had occupied these regions almost completely by the year 1937 (Fig. 12). The only difference is that in these provinces the muskrat populations have at almost all times been a little larger than in the country as a whole. However, in the worst low (1944) the populations in these provinces became distinctly smaller than elsewhere. (The discrepant value for the populations in the province of Häme in 1940 is based on exceptionally few notes and is therefore unreliable.)

The official statistics for catches also reveal changes in the muskrat stocks (Artimo 1953). The numbers of animals caught increased abruptly up to the year 1937 (Fig. 39). The catches then decreased equally abruptly until the low of 1944. In 1945, muskrats were protected. After 1947, a sharp rise occurred in the numbers caught; this persisted until 1950, being then followed by a period of rapid decline until 1953. In 1954 muskrats were again protected and in the spring of 1955 a new record catch was achieved (over 600 000), which was 2.5 times as great as the maximum catches in 1937 and 1950. In spring 1956, the catch then decreased to $^1/_3$ of the numbers trapped in the foregoing spring and the decrease continued in the year 1957; the catch increased in 1958 and decreased again in 1959.

When discussing the reliability of the inquiries concerning the changes in populations made by the Finnish Game Research Institute, Siivonen (1951) showed that when the figures for abundance, e.g. of the snow hare, capercaillie and black game, obtained from the game inquiry were 1.01—1.50 the catches were 1.5—2.5 specimens per 10 sq.km. When the figures rose to 1.51—2.00 the catches amounted to double this value (4—5 specimens per 10 sq.km.), when the figure increased still further to 2.01—2.50, the catches increased threefold (8—9 specimens per 10 sq.km.). Evidently, by analogy, both the rises and the falls are magnified in the statistics for muskrat catches (Fig. 39). These same differences may be still further exaggerated by the changes in the intensity of muskrat trapping. Already in autumn and winter trappers can estimate the probable catch the following spring from the numbers of winter houses. If the population seems to have decreased considerably, the profitableness of trapping

becomes questionable and it will not be undertaken with such intensity as when good results are anticipated.

The following essential features can be observed in the growth of Finnish muskrat populations. The growth of the population has occurred in two phases. There was a first phase of rapid increase up to the year 1937 resembling the phase of logarithmic growth of populations. Elton, e.g., (1949: 111) says: »Many of the most striking cases of sudden increase in animals occur when a species is introduced into a country strange to it. . .». From 1938, there followed a distinct phase of decline lasting for 7 years (with small rises between). Thereafter the phase of logarithmic growth continued again, beginning from the year 1944, and reached its peak in the record abundance and record catches of the year 1955. Then a new phase of decline set in. Had the populations in the year in question perhaps already reached their maximum density? It is still too early to draw any final conclusions, because it is not yet known how dense muskrat populations can become in favourable conditions in Finland. Nor can we say with certainty whether our muskrat stocks have already reached the state characterized by normal fluctuations, i.e. whether muskrats can be considered to have finally become acclimatized in Finland. In the springs of 1954 and 1955 muskrat populations were already so abundant that they caused considerable local destruction of the aquatic vegetation. Thus it would seem that the populations can hardly become much more abundant without seriously threatening their food resources. It thus seems that in the muskrat acclimatization can be said to have almost reached its final phase in Finland.

From catch statistics Innis (1927: 35) demonstrated that fluctuations in numbers of Canadian muskrats show a 10-year periodicity. Later Elton & Nicholson (1942) analyzed these and more recent Canadian catch statistics in detail and cames to the same conclusion. In muskrats, however, the periodicity is less distinct than in the Canadian hare (cf. also Errington 1951, 1954 b). Because the logarithmic growth period in Finland was interrupted by a decline lasting many years, it might be thought that this was dependent on periodicity (cf. Artimo 1945, 1949, 1953). Owing to the shortness of the observation period, however, it cannot be decided whether or not a similar 10-year periodicity occurs in Finland. In the Soviet Union, Lavrov (1955 a) has not yet been able to verify this type of periodicity in muskrats either.

B. Catches

At first, muskrats were looked upon with disfavour owing to their habit of digging in shores and banks, and on account of the destruction they caused to the fish nets and to the aquatic vegetation. Nests were destroyed on purpose in

many localities. Severe damage caused by muskrats was feared as a result of alarming reports from Central Europe (e.g. Liro 1924, 1925) and trapping was at first permitted throughout the year.

In 1934, an inquiry was made by the Ministry of Agriculture in order to investigate the damage inflicted by muskrats and the profitableness of muskrat trapping (Klemola 1937 b). This clearly demonstrated that people had learned the value of the muskrat as a fur-bearer. As complaints of the damage turned out to be greatly exaggerated, a close season every year from May 15 to December 31 was declared (Feb. 8, 1935). In 1938, muskrats were totally protected and thereafter trapping has been allowed during a short time from the end of April to the beginning of May. In Lapland and North Finland and in certain provinces of Central Finland the trapping season has generally been about one month longer than elsewhere in the country. In 1945 and 1954 muskrats were totally protected throughout Finland, and in 1947 in Lapland.

As muskrats spread and the populations increased in size, trapping became more intensive. In the war years (1940—1945) the number of trappers was considerably reduced and this may have significantly affected the size of catches. In the Soviet Union the same circumstance may have diminished the catches during these years (Semenov 1950, Lavrov 1955 a). In central Europe, effective trapping has caused a decrease in the numbers caught (Hoffmann 1958: 191—195). This source of error, however, does not affect the curve of the abundance of muskrats, because the reports on which this is based are sent in before the trapping season. It must also be borne in mind that the abundance of populations and the catch statistics had already decreased before the war. After 1945, muskrat stocks and catches increased. The number of trappers also increased, simultaneously, however, because the post-war depression and hope of easy money lured many trappers to muskrat shores. Yet both in the 1930's and in the 1940's, after the war, and at the beginning of 1950's the muskrat stocks and catches increased in spite of intensive trapping. Hence trapping has obviously not been so efficient as to account for the fluctuations noted in the muskrat populations throughout the country. The same conclusion was drawn by Pirnie (1941) on the basis of studies made in Ohio, Southern Ontario and Michigan.

After their protection in 1945 and in 1954, muskrat stocks have likewise become distinctly stronger and catches have increased. From this, it might be concluded that protection significantly promoted the increase of populations. The protection in the year 1945, however, came into force at a time when the increase of muskrat populations had already started in many localities. The worst phase of decline was already over (Artimo 1945). In spite of protection, poaching was very common and the effectiveness of the measure became very

questionable. In the year 1954 protection was quite unnecessary and came in for very severe criticism in fur circles, for in that year muskrat stocks were very abundant in many localities. Here, too, it is doubtful whether protection was beneficial. The populations were so abundant that even without protection they might have been able to reach the peak of 1955. The effect of trapping and protection upon the development of muskrat stocks is thus difficult to assess.

C. Hydrographic factors

Muskrats thrive best in watercourses where the water-level is relatively stable (pp. 41—42). The regulation of water-level has been shown to promote the growth of muskrat populations (pp. 50—51).

There have been many observations on the harmful effect of unfavourable water conditions upon muskrats (Anonymous 1935, Brander 1951 b).

At the Porla Fish Cultivation Station in Lohja, the following observations were made in Aug.—Sept. 1950. The muskrats living on a shore successively lengthened their trail leading from the bank to the water. On Aug. 1, the end of the trail at the highwater line was on dry land, about 5 m. from the shore bank. On Aug. 15, when the water-level had fallen lower, the trail ended at a distance of about 10 m. from the bank, on Aug. 30, at 17 m. and on Sept. 15, at 25 m. from the bank. As the water-level changed the muskrats continued to lengthen their trail and its end was visible on the days in question as a small widening. The new trail branched off from the end of the previous trail a little sidewards. Finally, when the water-level sank still lower, the muskrats had to move away.

Many reports (GRI) made in different years contain information on the effect of changes in water-level upon muskrat populations:

A number of muskrats died in the winter of 1929 in Luopioinen because the water-level was unusually low and the plunge-holes had frozen (V. Korvenkontio). E. Perkkola reported that in the Saimaa basin region the water-level in 1946 was noticeably lower during the summer also. In shallow-shored lakes (e.g. Puruvesi) some of the houses were left on dry land. The animals had to dig passages as much as 100 m. long. The muskrats decreased considerably in numbers. A. Pantzar (Dec. 26, 1946) wrote from Kyyvesi that the preceding winter had been a hard one for muskrats. The water-level had fallen and the passages froze to the bottom, many muskrats died in their houses and in summer many dead muskrats were found. The mortality was very heavy, especially in shallow bays. U. Koivula (1946) stated that in such lakes as Vanajavesi, where the fluctuation of the water-level is 2 m., muskrats had difficulty in getting to the water from their bank dens in the winter. Whole litters had been found dead in bank dens. Likewise spring floods drove the muskrats away from their nests. From Karjalohja P. Jalava (Jan. 11, 1947) reported that in the autumn of 1946 the muskrat was abundant. There was little water in winter and many of the nests were frozen. Movements of muskrats on the ice were observed, as they looked for openings. From Ruovesi L. Merisalo reported that in the winter of 1946/47 muskrats stocks suffered from the fall in the water-level and many died. The same winter there were many similar reports from other localities, and correspondingly for other winters. From Tyrvää A. Lounamaa reported that in December 1938 the water in the Kokemäenjoki basin rose by about 2 m. The muskrat bank dens filled with water, the openings of the burrows froze, and the animals were trapped inside. In the spring numerous dead muskrats were found in the water. J. Raekallio wrote that in the winter of 1937/38 muskrats abandoned the shores of lake Ladoga and its archipelago after having been very common in bays rich in vegetation, emigrating along streams and even to small ponds. The cause was a lowering of the water-level of Lake Ladoga by 40 cm. The vegetation was left

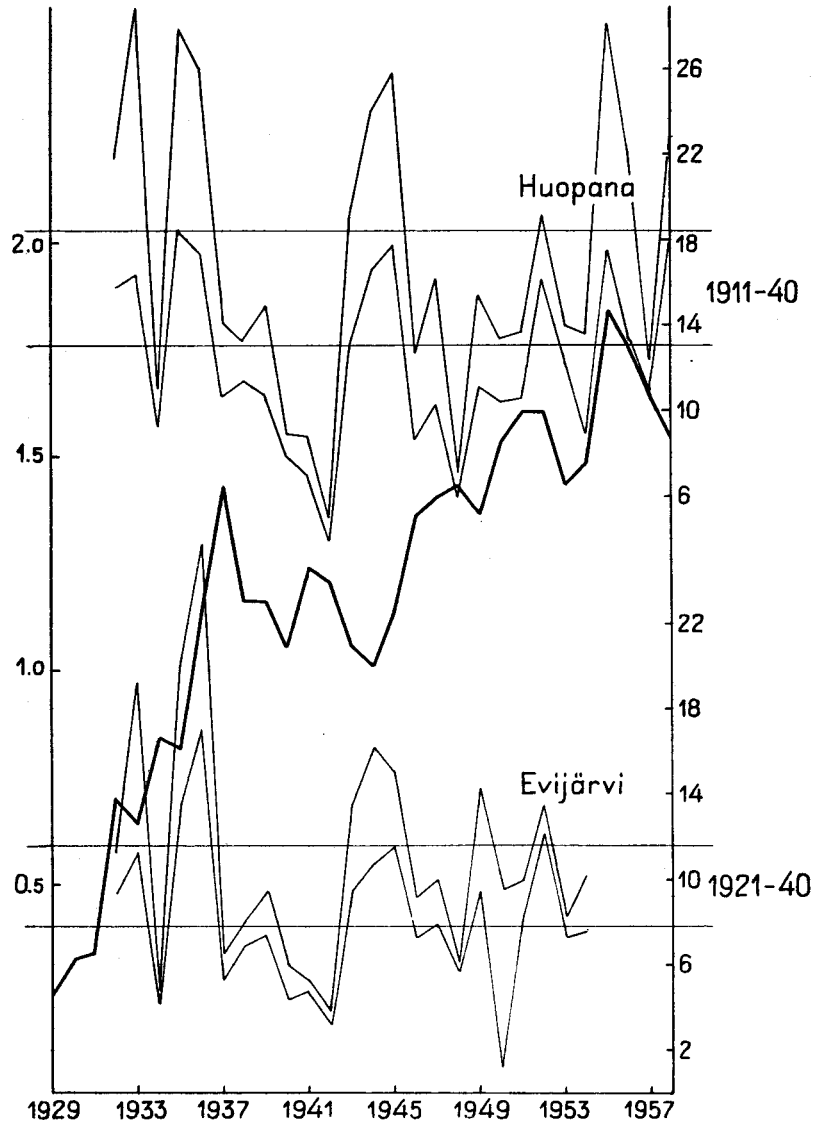

Fig. 40. The growth of the muskrat population in the entire country (in the middle, scale at left) and the variation in discharge from Huopana Rapids and Lake Evijärvi (cub. m./sec., scales at right) in January-March. The area between the parallel lines: the average variation in discharge.

high and dry and on account of the hard winter the water froze deep. I. Kekäläinen wrote (March 15, 1950) that in the autumn on 1950, owing to the high water-level, muskrats built their bank dens higher up the shores in Rautavaara, but the nests froze in winter and the muskrats perished. K. Soininen (May 14, 1954) stated that in Lylyisjärvi, Suonenjoki, 40 bank

dens were marked in autumn. Next spring the trappers observed that the whole muskrat population had been destroyed. The water had risen 1 m. during the winter and this caused their destruction.

Muskrats are in some degree able to adapt themselves to the changes in water-level at least during the season of open water (cf. e.g. p. 72). During dry seasons and when the discharge is small and when driven by unsually severe spring and autumn floods, muskrats have been observed to move to more suitable shores. Great changes, however, especially when they occur in late winter, can have a very destructive effect on local populations.

Changes in the discharge (cub.m./sec.) in the Huopana Rapids in the years 1932—54 during the most critical period of the year presented in Figure 40 (Yearbooks of the Hydrographic Bureau 10—15. In addition, later unpublished data were kindly placed at the authors' disposal). It illustrates the situation in typical parts of Lake-Finland. The other diagram shows the situation for Evijärvi, i.e. from the coastal region with rivers. On the basis of the annual reports of the Hydrographic Bureau of Finland it can be established that similar situations have arisen in different years in all parts of the country. During the period 1932—37 when the muskrat populations were increasing rapidly, the discharges in the Huopana Rapids and Lake Evijärvi were greater than normal. The late winter of 1934, with a very low discharge, was exceptional, but it did not affect the continuous increase of the muskrat populations. In spring 1937 the discharges were distinctly below normal but the muskrat populations were nevertheless at a maximum and record catches were obtained. Now followed a low-water period lasting many years, and throughout this time until 1942 the muskrat stocks were small. In the springs of 1943—45 the discharge was a little higher than normal, but the muskrat populations continued to decrease in numbers towards the low of 1945. Since then, the fluctuations in the discharge have been fairly normal (Evijärvi) or a little smaller than normal (Huopana) and the muskrat populations have again increased. In the spring of 1950, when the catches were good, the discharge in late winter was small and the fluctuations, especially in Lake Evijärvi, very great indeed.

Although an unfavourable water situation may cause great losses in muskrat populations, they probably had no really harmful effect on muskrat stocks in Finland. Evidently the fluctuations in discharge have been so slight that their injurious effect has been restricted to local cases, chiefly to shallow shores where even small fluctuations are significant.

The decline after 1937 took place during a period characterized by a most unfavourable water situation which, coinciding with other detrimental factors, may even have resulted in losses, whereas the new period of increase from 1945 onwards took place at a time when the water situation in late winter was generally fairly favourable.

D. Winter conditions

During severe winters, the danger of total freezing of watercourses is very great, particularly on shallow shores where foraging will then be more difficult and the muskrats may die of hunger (e.g. Cox 1936, Hamerstrom & Blake 1939, Aldous 1947). If under such circumstances they move to other watercourses in search of open waters, as has often been observed, they frequently perish (Osgood 1938, Smith 1938, Highby 1941, Errington 1939 a, 1940, 1941, Porshild 1945, Gashwiler 1948, Rand 1948). Observations on the destructive effect of severe winters up on muskrat stocks have been made in Central Europe and in the Soviet Union, too (Semenov 1950, Hoffmann 1958, Karpukhin 1958).

The essential significance of the winter conditions is demonstrated by numerous records filed in the archives of the Game Research Institute.

N. Hernemaa, of Lehtimäki, reported that in winter 1949/50 the ground was unfrozen and then came a frost of —30° C, the ground and water freezing to a depth of ½ m. The muskrats moved away to search for open water but died on the way. Numerous dead muskrats were found that winter. T. Sovinen, of Varkaus, wrote that in January 1950 a car ran over a muskrat in the middle of the market-town of Varkaus. E. Korpi, of Multia, reported that a muskrat was found on January 5, running on the ice. O. Vohlonen, of Oulunsalo, stated that at the end of February 1950 a muskrat was living in his neighbour's barnyard, which was 800 m from a lake. M. Rintasalo, Ilmajoki, reported that in the winter of 1949/50 muskrats had to move from some clay pools because these froze to the bottom. One specimen was killed in a grain store 500 m. from the nearest pool, which was dry. A muskrat stiff with cold was run over by a vehicle in January 1950. T. Mäki, Humppila, reported that on Jan. 1, 1950, a muskrat was found on the snow in a field. V. Webor, Juva, stated that after severe frosts in the winter of 1950 muskrats were seen moving over the ice and in the woods. T. Auvinen, Korpilahti, stated that in winter 1950 muskrats were seen running on the ice and many specimens were found frozen to death. T. Nieminen, of Keuruu, found two dead muskrats on the ice. W. Blom, of Koskenpää, saw muskrats on the ice in the beginning of February. In January—March, 1950, V. Mikkola, of Rääkkylä, observed muskrats moving on the ice. T. Hämäläinen, of Rautalampi, saw unsually large numbers of muskrats moving on the ice. T. Karjalainen, of Siikajoki, reported that between Feb. 8— Feb. 22, 1950, movements of muskrats on the ice were very common. F. Yli-Länttä, of Ullava, found one dead muskrat on the ice in March 1950. In January E. Halmesmäki, of Viitasaari, noted unusual movement of muskrats on the ice of small lakes. J. Huttunen, of Vesanto, reported that muskrats abandoned shallow ponds during the period Jan. 15 — Feb. 10, 1950, I. Kekäläinen, of Rautavaara, stated that the winter of 1950 was destructive to muskrats. The nests were frozen. In January 1950, a muskrat was found in the larder of a house. At the beginning of February, 1950, U. Finnär, of Ähtävä, observed signs of a group consisting of 5 muskrats in a forest many kilometres from the lake. Single specimens were found near villages where they were taken for rats and killed. H. Seppälä, Lappajärvi, reports that in the autumn of 1949 muskrats were exceptionally numerous in Lake Menkijärvi. There was little snow that winter but severe cold spells in which the shallow bays froze to the bottom, and the winter houses were also frozen. At least 4 specimens could be verified to have moved away. Two specimens were found dead and decayed on a lake shore 4.3 km. northeast of Lake Lappajärvi. Previously a catch amounting to several dozens was trapped from the lake, but in spring only one specimen was caught. In winter 1949/50 O. Häggblom, Lappajärvi, found 2 muskrats dead ½ km. from the shore of the lake.

Of the various factors possibly causing winter mortality in muskrat populations, the fluctuations in the length of the time when the watercourses are under

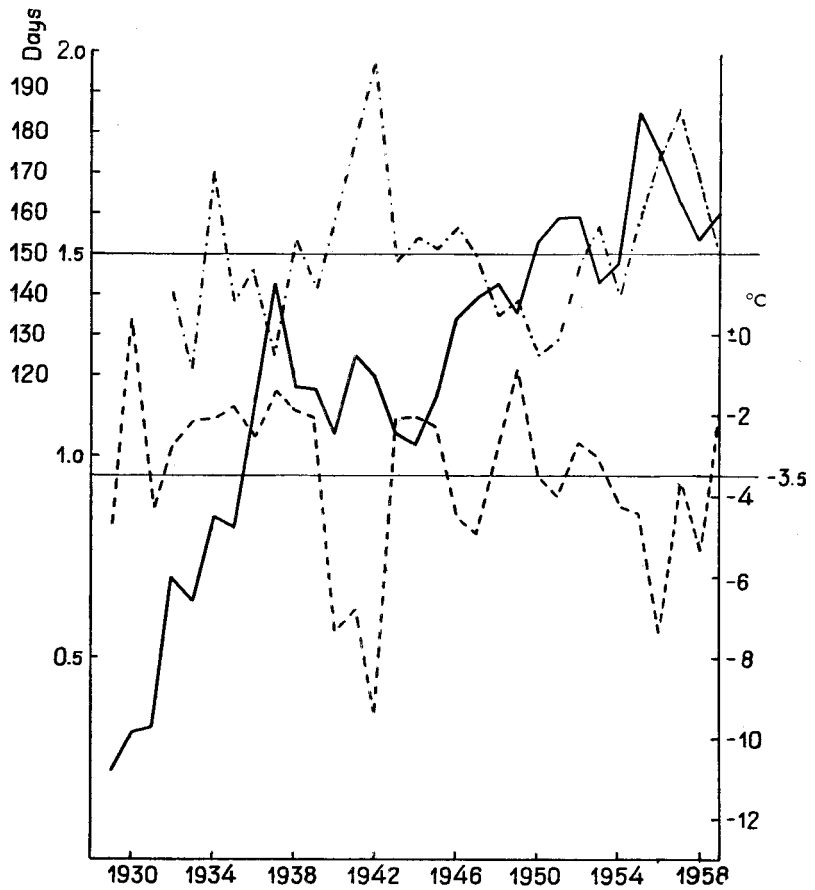

Fig. 41. The fluctuation of the muskrat population in the entire country (———) and the lenghts of the ice period in the district of Roine-Längelmävesi (area IX) in the winters of 1931/32—1958/59 (— • — • —) and the mean temperature of winter period (XI—IV) in Tampere in 1929/30—1958/59.

ice seem to show the greatest correlations with changes taking place. In Figure 41 the fluctuations in the length of this time in the area IX (Fig. 2), during the winters of 1931/32—1958/59 are presented (on the basis of data in Yearbooks of the Hydrographic Bureau).

From the diagrams it can be seen that relatively shorter winters preceded the first period of increase in muskrat populations (only the winter of 1933/34 was clearly longer than the normal one, 150 days), Thus the peak in 1937 followed a short winter. The period of decrease which started in 1938 occurred after a winter

which was longer than normal. The winters of the regression period which then set in were considerably longer than normal. The new phase of population increase after the winter of 1944/45 began when winters of about normal length prevailed. When the cold period again lengthened (in the winters of 1955/56 and 1956/57), the muskrat populations became distinctly smaller.

In Lapland, where the length of the winter is approximately 210 days, muskrats prefer living in streams (p. 51) which are the most favourable biotopes during the winter.

In spite of the distinct correlation between the length of the winter and the changes in muskrat populations, other factors acting during this time seem also to influence the outcome.

The mean temperatures of the winter period (XI—IV) and the normal means in Tampere (area IX; Monthly Surveys of the Meteological Office 1928—59) are presented, too (Fig. 41). The climatic conditions in this region give a good idea of the situation in those areas where our muskrat stocks are most abundant.

In the winters of 1931/32—1954/55 the mean temperature fluctuated fairly evenly around the normal one (—3.5° C). The first phase of increase in muskrat populations occurred during mild winters. In the years 1940—1942 losses took place during the very severe winters. The muskrat populations then continued to decrease, it is true, even through the temperature became noticeably more favourable. After the low of 1944 the muskrat stocks became more abundant. During this time the winter temperatures fluctuated around the normal, i.e. there were mild winters.

An examination of the relation of winter temperatures and trends in muskrat populations indicates that only the severest winters have been able to diminish the muskrat stocks, as obviously happened during the winters of 1939/40—1941/42 (cf. Merisalo 1944). The fluctuations in winter temperatures at least within the limits occurring in Finland have evidently not affected the muskrat stocks except perhaps locally on low shores and shallow lakes. This seems very natural, for muskrats thrive in their native country in its northernmost parts in regions where the temperature in winter is regularly lower. Likewise it has been observed that muskrats thrive in Siberian watercourses (e.g. Bujacovič 1951, Lavrov 1955 b, 1957) where the winter are far colder than in Finland.

The insulating effect of the snow cover is essential for the thriving and survival of many small animals over the winter (e.g. Formosov 1939, Farsky & Mrkos 1942). A thick snow cover completes the protection that bank dens or muskrat houses give to muskrats in winter. Severe winters with a thin snow cover are known by trappers to be very harmful to muskrat stocks. Porshild (1945) remarks that »is is important for the rat that an abundant snow covers the lakes and the

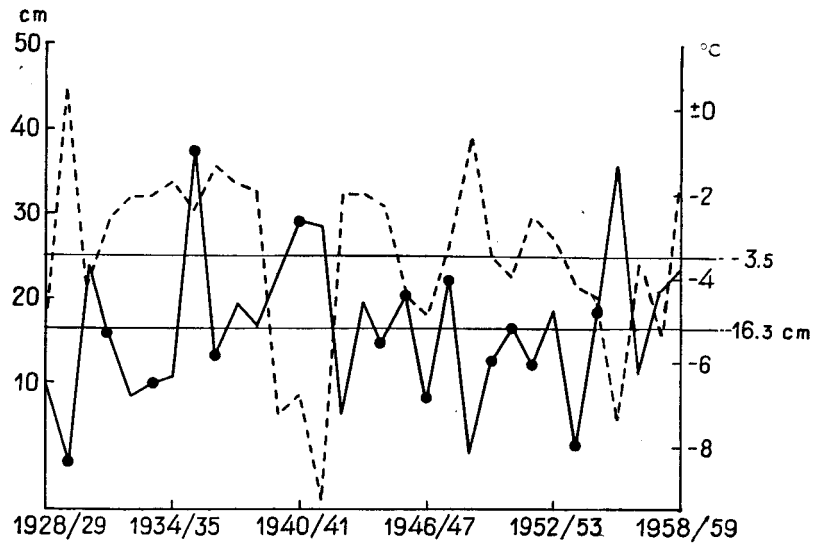

Fig. 42. The relation between the mean temperature (– – –) of the winter period (XI—IV) in Tampere, depth of snow cover (———) and success of overwintering (● = after the winter the muskrat populations were larger).

push ups.» In Minnesota attempts are made to avoid great losses in winter by giving a far greater number of trapping licenses in winters with thin snow cover than in winters with abundant snow (Highby 1941).

The depth of the snow cover in the Tampere district in the winters of 1928/29—1958/59 (Monthly Surveys of the Meteorological Office 1928—59) is shown in Figure 42. The mean depth of the snow cover in the period in question was 16.3 cm. When possible, the effects of depth of snow cover on the survival of muskrat populations over the winter have been examined, and it was found that after the rather cold but short winter of 1935/36 with thick snow, the numbers of muskrats rose and catches increased. After the following mild winter with less snow the muskrats became even more abundant. Later there were many winters (1937/38—1941/42) when cover was thicker but at the same time the temperatures were lower and the populations declined. Even the exceptionally thick snow cover could not prevent the decline of the populations and their decrease to a minimum. The depth of the snow cover in the following winters fluctuated round its average value, but in many winters was below this. The muskrat stocks, however, became more abundant (with phases of slight decrease) and reached a new maximum in spring 1955, although winter temperatures continued to be very low. The thinness of the snow cover had not yet had any adverse effect on the growth of the muskrat populations.

Hence, although a thick snow cover in winter, which is often accompanied by severe frosts, has in certain winters been able to protect our muskrat stocks from greater losses, no correlation can be discerned between the thickness of the snow cover and the success of overwintering of the muskrat populations.

VI. SUMMARY

For economic reasons, a total of about 1100 muskrats were imported into Finland from Germany, Czechoslovakia, and North America. Muskrats reared on fur farms here and specimens caught from nature were also used for introductions. Muskrats were released in a total of 293 localities from Hankoniemi to Inari. The total number of specimens introduced amounted to about 2300.

The dispersion from the centres of release was very rapid. Within about 35 years (1920—55) muskrats had occupied virtually all those watercourses generally capable of supporting them. Only in the drainage basin of the Rivers Tornion — Muonionjoki have they perhaps further possibilities to spread to any great extent.

The present limit of the distributional area of muskrats runs through the watershed were the Kemijoki drainage basin has its sources and in the drainage basin of the Rivers Tornion — Muonionjoki in Muonio, to which they have recently extended their range.

In North Finland spread has been distinctly slower than in the southern and central parts of the country. The speed of emigration has varied in South and Central Finland between the limits of 4—120 sq.km./year. The usual values have been 10—20 km./year. Compared with other mammals, this speed is very great. The rate of spreading has varied between the limits of 4—170 sq.km./year. In the watercourses of the coast, which consist mainly of rivers, the average rates of spreading have been distinctly lower (4—15 sq.km./year) than inland, in the lake district (25—50 sq.km./year). The results are the same even if only the littoral zone is reckoned as the area occupied. This may depend on the fact that lakes are open biotopes in which dispersion is always possible in almost every direction, whereas rivers are closed biotopes, dispersion having limited possibilities and the central area soon becoming overpopulated.

The number of muskrats released seems not to have had any essential effect on the rate of dispersion.

The Virginian muskrat has not done so well in Finland as the nominate race. The spread observed at the beginning soon ceased and the animals have disappeared altogether from many of the sites of release. The largest continuous area is at present in the Saimaa district.

The climatic similarities between the native areas of the nominate race in the Great Lakes region of North America and in Finland has been the main factor accounting for the successful introduction of muskrats into this country. The poor thriving of Virginian muskrats must also depend on the fact that the climate of its native range deviates noticeably from that of Finland.

The normal annual variations of water-level in Finland are not so great as to affect the muskrats adversely. On shallow shores, in the northern parts of Pohjanmaa and on both sides of the Bay of Viipuri, the variation in water level is so great that muskrats have not settled down there.

Muskrats have been observed to thrive best in eutrophic and dys-eutrophic lakes where food is plentiful. Such localities are commonest in South and S.W. Finland where agriculture is more intensive. Dystrophic and oligotrophic lakes are distinctly less productive. The last-mentioned waters do not generally harbour permanent muskrat populations.

In very shallow lakes which freeze to the bottom in winter muskrats do not succeed. Nor do they like very steep shores with narrow zones of aquatic vegetation.

The nature of the shores also determines the suitability of a locality. For this reason muskrats do not normally colonize bogs although they have rapidly occupied ditches dug in them.

As between flowing and standing water, muskrats show no preference.

Small watercourses where the factors of erosion have little effect on the shores and aquatic vegetation, are the best muskrat habitats.

Salinity or pollution of the waters seems to have no harmful effect on muskrat populations.

The favourite food plants of muskrats are: *Typha, Sparganium erectum, Scirpus lacustris, Carex* spp., *Equisetum limosum, Isoëtes, Sparganium simplex* and *Phragmites*. Plants with floating leaves are also important food plants.

The aquatic vegetation available to muskrats in Finland is very similar to the plants to which the species is accustomed in its native country. In this respect, muskrats have come to an environment familiar to them. The same may be said of their animal food, which muskrats have been shown to use more in the cold season. The best conditions regarding their plant food productivity prevail in the southern and central parts of the country. The barrenness of the waters of North Finland has prevented the occupation of watercourses there.

In watercourses occupied by dense muskrat populations the disappearence of aquatic vegetation has been distinctly discernible as a result of muskrat activity. Horstail rush, common reed, and bulrush stands (*Equisetum, Phragmites,* and *Scirpus* associations) have suffered the most serious depredations from muskrats.

The disappearance of aquatic vegetation has only continued up to a certain point, however. The balance between the muskrat density and aquatic vegetation is evidently reached fairly soon.

No competition in regard to food or space has been observed between muskrats and other mammals living in Finnish watercourses. No species occupying a similar ecological niche live in our shore biotopes. In this respect these have been open to muskrats. This has certainly been one of the main factors responsible for the quick spread of these animals.

In Finland, muskrats have the same (or at least closely related) enemies as in their native country. It has not been established that their predators have in any way been able to limit the spread and acclimatization of muskrats.

In the first years after their introduction muskrats more generally gave birth to their young in muskrat houses than they do at present. But evidently the destruction of their houses, chiefly by man, has led to a decrease in this habit and nesting in bank dens has become more general. This phenomenon has been so common that a change of nesting habit occurring in connection of acclimatization can be spoken of.

Sexual maturity is only attained by muskrats in the spring after their year of birth.

The number of litters according to observations in the southern parts of country, is two, and sometimes only one.

The number of embryos varies in muskrats from 1 to 10, the average being 6.8. The number of young also varies within the same limits, the average being 4.8.

The logarithmic growth period of muskrat stocks in this country has been biphasic. Up to 1937 there was a rapid increase. Then followed a phase of decline lasting 7 years, after which the populations increased up to the year 1955, when the highest peak was reached. Since then the populations have been decreasing, but it cannot be said whether the muskrat stocks have already reached the maximum abundance compatible with carrying capacity.

The extent of catches, on the scale carried out here, has not been able to affect the variations occurring in the populations.

Unfavourable water conditions have sometimes caused great changes in local populations but they have evidently had no fundamental effect on muskrat population trends in the entire country.

The winter is the period when the muskrats are most vulnerable. The length of the ice period was observed to be the main factor responsible for the decline occurring after 1937 and for the fact that the growth phase of the population has been biphasic.

VII. LITERATURE

AHONEN, V., 1924, Ylivieskaan istutetut piisamirotat. — Metsästys ja Kalastus 13: 193—194.
— 1928, Brev från Ylivieska. — Tidskr. f. Jakt och Fiske 11: 478—481.
AIRAKSINEN, K., 1927, Vieläkin piisamimyyrästä. — Metsästys ja Kalastus 16: 81—84.
ALDOUS, S. A., 1947, Muskrat trapping on Sand Lake National Wildlife Refuge, South Dakota. — Jour. Wildl. Mgt. 11: 77—90.
ALT, E., 1932, Klimakunde von Mittel- und Südeuropa. (KÖPPEN, W. und R. GEIGER, Handbuch d. Klimatologie III, M.) — Berlin.
ANDERSON, W. L., 1948, Level ditching to improve muskrats marshes. — Jour. Wildl. Mgt. 12: 172—176.
ANDTBACKA, A. W., 1923, Import av bisamråttor. — Finlands Jakttidskrift 18: 45.
— 1924, Bisamråttorna. — Finlands Jakt & Fisketidskrift 19: 30—31.
ANONYMOUS, 1925a, Piisamimyyrä Hauholla ja Tuuloksessa. — Suomen Kalastuslehti 32: 63—64.
— 1925b, Piisamimyyrä Hämeenlinnassa ja Tampereen seuduilla. — Ibid. 32: 152.
— 1928a, Piisamimyyrä Helsingissä. — Metsästys ja Kalastus 17: 199—200.
— 1928b, Gott om bisamråttor i Kyrkslätt. — Tidskrift f. Jakt och Fiske 11: 565.
— 1929, Bisamråttan i Lempäälä socken. — Ibid. 12: 199—200.
— 1930a, Piisamimyyrä leviää. — Metsästys ja Kalastus 19: 93.
— 1930b, Bisamråttor i havsbandet. — Fiskeritidskr. f. Finland 35: 75—76.
— 1935, Piisamimyyrästä voi tulla vesiemme arvokkain riistaeläin. — Metsälehti 1935: 42, 7.
— 1950, Eräiden riistaeläinten nykyinen esiintyminen maassamme. — Luonnon Tutkija 54: 94—96.
ANTHONY, H. E., 1935, Field book of North American Mammals. — New York—London.
ARATA, A. A., 1959, Ecology of muskrats in strip-mine ponds in southern Illinois. — Jour. Wildl. Mgt. 23: 177—186.
ARTHUR, S. C., 1928, The fur animals of Louisiana. — Bull. 18 of the Dept. of Conserv. New Orleans.
ARTIMO, A., 1945, Piisamimyyrän esiintyminen maassamme. — Luonnon Ystävä 49: 177—178.
— 1949, Suomi tuottavana piisamimaana. (Summary: Finland as a profitable muskrat land.) — Suomen Riista 4: 7—61.
— 1952, Om de spår bisamråttan lämnar i naturen. (Summary: Singns of muskrat.) — Pap. Game Res. 8: 63—76.
— 1953, Piisamisaaliiden vaihtelut Suomessa. (Summary: On the fluctuations in the harvest of the muskrat.) — Suomen Riista, 8: 180—181, 232—233.
— 1956, Piisami. (SIIVONEN, L., Suuri nisäkäskirja, Mammalia Fennica pp. 467—486.) — Helsinki.
— 1957, Piisamin luontaisesta ravinnosta. (Summary: On the natural nourishment of muskrat.) — Suomen Riista 11: 109—122.
BACHRACH, M., 1930, Fur. A practical treatise. — London.
BAILEY, B., 1929, Mammals of Sherburne County, Minnesota. — Jour. Mammal. 10: 153—164.
BAILEY, V., 1937, The Maryland muskrat marshes. — Ibid. 18: 350—354.
BEDNARIK, K., 1956, Muskrat in Ohio Lake Erie marshes. — Div. Wildl. Ohio Dept. of Nat. Res. Columbus 12, Ohio. 67 pp.
BEER, F. R., 1950, The reproductive cycle of the muskrat in Wisconsin. — Jour. Wildl. Mgt. 14: 151—156.
— & W. TRUAX, 1950, Sex and age ratios in Wisconsin muskrats. — Ibid. 14: 323—331.
BELLROSE, F. C. Jr., 1950, The relationship on muskrat populations to various marsh and aquatic plants. — Ibid. 14: 299—315.
— & L. G. BROWN, 1941, The effect of fluctuating water levels on the muskrat population of the Illinois River Valley. — Ibid. 5 :206—212.
— & J. B. LOW, 1943, The influence of flood and low water levels on the survival of muskrats. — Jour. Mammal. 24: 173—188.

BERGSTRÖM, U., 1948, Smågnagarna. (Svenska Djur, Däggdjuren pp. 385—444.) — Stockholm.
BORELL, A. E., & R. ELLIS, 1934, Mammals of the Ruby Mountains Region of north-eastern Nevada. — Jour. Mammal. 15: 12—44.
BRANDER, T., 1949, Om bisamråttan i Finland ur naturskyddssynpunkt. — Finlands Natur 8: 12—23.
— 1950a, Piisamimyyrän rakennustaituruutta. — Metsästys ja Kalastus 39: 122—125.
— 1950b, Miten voimme lisätä maamme piisamituottoa. — Ibid. 39: 297—300.
— 1951a, Tre studier över bisamråttan (Ondatra z. zibethica L.). — Acta Soc. F.Fl. Fenn. 67, 3: 1—54.
— 1951b, Om bisamråttan ur jaktvårdssynpunkt. (Summary: On the muskrat from the point of wiew of game management.) — Finskt Villebråd 5B: 84—142.
— 1951c, Bidrag till kännedom om bisamråttans (Ondatra z. zibethica L.) kägelbobyggen. — Mem. Soc. F. Fl. Fenn. 26: 32—37.
— 1955a, Über die Bisamratte, Ondatra zibethica (L.), als Vernichter von Najaden. — Arch. f. Hydrobiol. 50: 92—103.
— 1955b, Weitere Beobachtungen zur Muscheldiät der Bisamratte. — Ibid. 51: 261—266.
— 1956, Faunistisia ja floristisia muistiinpanoja Pyhäjokilaaksosta (OM) v. 1955. — Oulun Luonnonyst. Yhd. Julk. A, III, 4: 50—53.
BRANDER V., 1924, Är utplantering av bisamråttor välbetänkt? — Finlands Jakt & Fisketidskrift 19: 351.
BROFELDT, P., 1934, Piisamimyyrän vahingollisuudesta kalavesissä. — Turkistalous 6: 19—20.
BUJAKOVIC, N. G., 1951 Ондатра на крайнем северо-востоке Союза ССР. Зоол. журнал 30: 279—285.
BURT, W. H., 1948, The mammals of Michigan. — Univ. Mich. Press. Ann. Arbor.
BUTLER, L., 1940, A quantitative study of muskrat food. — Canad. Field Nat. 54: 37—40.
BÖÖK, A. TH., 1928, Piisamimyyrän leviäminen Hämeessä. — Luonnon Ystävä 32: 218.
CAHALANE, V. H., 1947, Mammals of North America. — New York.
CHAPPELIER, A., 1948, Le Rat musqué en France. — Bull. Franc. piscicult. 21: 137—158.
CONNOR, A. J., 1938, The climates of North America, Canada (KÖPPEN, W. und R. GEIGER, Handbuch der Klimatologie II, J: 2, 331—324). — Berlin .
COX, W. T., 1936, Snowshoe rabbit migration, tick infestation and weather cycles. — Jour. Mammal. 17: 216—221.
CROSMAN, J. B., 1927, Notes on the food of the red fox. — Bull. Boston Soc. Nat. Hist. 42: 8.
DAILEY, E. J., 1927, Practical muskrat raising. — Columbus, Ohio.
DALQUEST, W. W., 1948, Mammals of Washington. — Univ. Kansas Public. Mus. Nat. Hist. 2, 1: 1—444.
DIXON, J., 1922, Rodents and reclamation in the Imperial Valley. — Jour. Mammal. 3: 136—146.
DORNEY, R. S. & A. J. RUSCH, 1953, Muskrat gowth and litter production. — Technical Wildl. Bull. 8. Wisc. Conserv. Dept. 32 pp.
DOZIER, H. L., 1945, Sex ratio and weights of muskrats from the Montezuma National Wildl. Refuge. — Jour. Wildl. Magt. 9: 232—237.
— 1947, Salinity as a factor in Atlantic coast tidewater muskrat production. — Trans. N. Am. Wildl. Conf. 12: 398—420.
— 1948a, Color mutations in the muskrat (Ondatra z. macrodon) and their inheritance. — Jour. Wildl. Magt. 20: 393—405.
— 1948b, Estimating muskrat populations by house count. — Trans. N. Am. Wildl. Conf. 13: 372—392.
— , M. H. MARKELEY, and L. M. LLEWELLYN, 1948, Muskrat investigations on the Blackwater National Wildlife Refuge, Maryland, 1941—1945. — Jour. Wildl. Mgt. 12: 177—190.
DURRANT, S. D., 1952, Mammals of Utah. — Univ. Kansas Publ. 6: 1—549.
ECKE, D. H., 1954, An invasion of Norway rats in Southwest Georgia. — Jour. Mammal. 35: 521—525.
ELTON, C., 1949, Animal ecology. — London.
— & M. Nicholson, 1942, Fluctuations in numbers of the muskrat (Ondatra zibethica) in Canada. — Jour. Animal Ecol. 11: 96—126.

ENDERS, R. K., 1932, Food of muskrat in summer. — Ohio Jour. Sci. 32: 21—30.
— 1939, The corpus luteum as an indicator of the breeding of muskrats. — Trans. N. Am. Wildl. Conf. 4: 631—634.
ERRINGTON, P. L., 1935, Food habits of Mid-West foxes. — Jour. Mammal. 16: 192—200.
— 1937a, Drowning as a cause of mortality in muskrats. — Ibid. 18: 497—500.
— 1937b, The breeding season of the muskrat in northwest-Iowa. — Ibid. 18: 333—337.
— 1937c, Food habits of Iowa foxes during a drought summer. — Ecology 18: 58—61.
— 1937d, Habitat requirements of stream-dwelling muskrats. — Trans. N. Am. Wildl. Conf. 2: 411—416.
— 1939a, Reactions of muskrat populations to drought. — Ibid. 20: 168—186.
— 1939b, Observations on young muskrats in Iowa. — Jour. Mammal. 20: 465—478.
— 1940, Natural restocking of muskrat-vacant habitats. — Jour. Wildl. Mgt. 4: 173—185.
— 1941, Versatility in feeding and population maintenance of the muskrat. — Ibid. 5: 68—89.
— 1943, An analysis of mink predation upon muskrats in north-central United States. — Iowa Agr. Exp. Sta. Res. Bull. 320: 797—924.
— 1946, Predation and vertebrate populations. — Quart. Rev. Biol. 21: 144—177, 221—245.
— 1948, Environmental control for increasing muskrat production. — Trans. N. Am. Wildl. Conf. 13: 596—609.
— 1951, Concerning fluctuations in population of the profilic and widely distributed muskrat. — Amer. Naturalist 85: 273—292.
— 1954a, The special responsiveness of mink to epizootics in muskrat populations. — Ecol. Monogr. 24: 377—393.
— 1954b, On the hazards of overemphasing numerical fluctuations in studies of 'cyclic' phenomena in muskrat populations. — Jour. Iowa Agric. Exp. St., Proj. 1217: 66—90.
— & T. G. SCOTT, 1945, Reduction in productivity of muskrat pelts on an Iowa marsh through depredation of red foxes. — Jour. Agric. Res. 71: 137—148.
FARSKY, O., & J. MRKOS, 1942, The influence of winter 1939/40 on the field mouse Microtus arvalis. — Ochrana Rostlin 18: 42—49. (Russ. According to Fortschr. Zool. 1945, 9: 50.)
FASSET, N C., 1940, A manual of aquatic plants. — New York—London.
FORBES, T. R., & R. K. ENDERS, 1940, Observations on corpora lutea in the ovaries of Maryland muskrats collected during the winter months. — Jour. Wildl. Mgt. 4: 169—172.
FORMOZOV, A. N., 1939, The snow covering as an environment factor and its importance in the ecology of mammals and birds. — Bull. Soc. Nat. Moscou, S. Biologique 48, 4: 60—69.
GASCHWILER, J. S., 1948, Maine muskrat investigations. — Bull. Maine Dept. Inland Fisheries and Game. 38 pp.
— 1950, A study of the reproductive capacity of Maine muskrats. — Jour. Mammal. 31: 180—185.
GERSCHENSON, S., 1945, Evolutionary studies on the distribution and dynamics of melanism in the hamster (Cricetus cricetus L.). I. Distribution of black hamster in the Ukrainian and Bashkirian Soviet Socialist Republics (USSR). — Genetics 30: 207—232.
GIBAN, J. et J. AUBRY, 1956, Extension actuelle du rat musqué en France. — Mammalia 20: 34—45.
GREENWELL, G. A., 1948, Wildlife values of Missouri farm ponds. — Trans. N.Am. Wildlife Conf. 13: 271—281.
GRIMM, W. C., & H. A. ROBERTS, 1950, Mammal survey of southwestern Pennsylvania. — Final Rep. Pittman—Robertson Proj. 24-R. Pennsylvanian Game Comm. Harrisburg, Pa. 99 pp.
HAKOLA, T. P., 1926, Piisamimyyristä Etelä-Hämeessä. — Suomen Kalastuslehti 33: 162—164.
— 1927, Vieläkin piisamimyyristä. — Ibid. 34: 170—171.
— 1931, Kevätkutuisten kalojen viljelyksestä Ruununmyllyn kalanviljelyslaitoksessa. — Ibid. 38: 125—127.
HALL, E. R., and E. L. COCKRUM, 1953, A synopsis of the North American Microtine Rodents. — Univ. Kansas Public., Mus. Nat. Hist. 5, 27: 373—498.
HALME, E., 1950, Die Abwasserfrage der Zellstoffwerke im Lichte einiger fischtoxikologischen Versuche. — Ann. Zool. Soc. Zool. — Bot. Fenn. 'Vanamo' 13, 7: 1—118.
HAMERSTROM, F. N. Jr., & J. BLAKE, 1939, Central Wisconsin muskrat study. — Am. Midland Nat. 21: 514—520.

HAMILTON, H. J., 1935, Notes on food of red foxes in New York and New England. — Jour. Mammal. 16: 16—21.
— 1939, American mammals, their lives, habits and economic relations. — New York and London.
— N. W. MOSLEY & A. E. MCGREGOR 1937, Late summer and early fall foods of the red fox in central Massachusetts. — Jour. Mammal. 18: 366—367.
HANNELIUS, H., 1948, Bisamråttan i Finland. — Svensk Jakt 85: 128.
HARJU, L., 1946, Piisamimyyrän tuhoja. — Metsästys ja Kalastus 35: 254.
HARRIS, T. van, 1952, Muskrats on tidal marshes of Dorchester County, Maryland. — Board of Nat. Res., Dept. of Res. and Educ. Publ. 91: 1—36. (According to Wildl. Res. 69, 2.)
HATFIELD, D. M., 1939, Winter food habits of foxes in Minnesota. — Jour. Mammal. 20: 258.
HEWITT, O. H., 1942, Management of an artificial marsh in southern Ontario for ducks and muskrats. — Trans. N.Am. Wildl. Conf. 7: 277—283.
HIGHBY, P. R., 1941, A management program for Minnesota muskrat. — Proc. Minn. Acad. Sci 9: 30—34.
HODGSON, R. G., 1924, Raising muskrats for profit. — Ontario.
— 1927, Succesful muskrat farming. — Toronto.
HOFFMANN, M., 1958, Die Bisamratte. — Leipzig.
HOLLISTER, N., 1911, A systematic synopsis of the muskrats. — N.Am. Fauna 32.
HÄPPOLÄ, L., 1928, Piisamimyyrien esiintymisestä Tuuloksessa. — Suomen Kalastuslehti 35: 74.
ILVESSALO, Y., 1929, Suomen päävesistöalueiden metsät. (Summary: The Forests of the main watershed areas of Suomi, Finnland.) — Metsätiet. Tutk. Laitoksen Julk. (Comm. Instit. Question. Forest. Finlandiae) 13: 1—154.
INNIS, H. A., 1927, The fur-trade of Canada. — Toronto.
JAKOWLEW, M. G., & I. M. KOLESNIKOV, 1954, Некоторые новые данные по распространению и экологии предкавказского хомяка в Ростовской области — Зоол. журнал 33: 693—700.
JOHNSON, V. E., 1925, The muskrat in New York. — Roosevelt Wildl. Bull. 3: 204—322.
JURVA, R., 1952, Seas. (Suomi, a general handbook on the geography of Finland, pp. 136—160.) — Helsinki.
JUVELIUS, I., 1926, Piisamimyyrä Kiuruvedellä. — Luonnon Ystävä 30: 87.
JÄRNEFELT, H., 1952, Limnological classification of Lakes. (Suomi, a general handbook on the geography of Finland, pp. 202—208.) — Helsinki.
— 1953, Välähdyksiä ihmisen sisävesillemme tuottamista vaurioista. — Kalataloussäätiön Julkaisuja 3: 1—7.
JÄRVI, T. H., 1911, Über den Krebs (Astacus fluviatilis Rond.) und die Krebsepidemieen in Finnland. — Acta F. Fl. Fenn. 33, 3: 1—41.
JÄRVINEN, A. E., 1950, Turkis- ja petoeläimet. (Suomen Metsästys pp. 153—158). — Helsinki.
KALABUKHOV, N. I., 1935, Закономерности массового размножения мышевидных грызунов. (Summary: On the causes of fluctuations in numbers of mouselike rodents.) — Зоол. Журнал 14: 209—242.
KALELA, O., 1938, Über die regionale Verteilung der Brutvogelfauna in Flussgebiet des Kokemäenjoki. — Ann. Zool. Soc. Zool. — Bot. Fenn. Vanamo 5, 9: 1—291.
— 1940, Über die Einwanderung und Verbreitung des Iltis, Putorius putorius (L) in Finnland. — Ann. Acad. Scient. Fenn. A, LIV, 6: 1—76.
— 1948, Hillerin levinneisyysalueen muutoksista Suomessa. (Summary: Changes in the distribution of the polecat in Finland.) — Suomen Riista 2: 77—96.
KARPUKHIN, I. P., 1958, О случаях гибели ондатры (Ondatra zibethica L.) на Колыме. (Summary: On the cases of ondatra perishing on Kolyma.) — Зоол. жуннал 37: 1575—1576.
KELLOG, C. E., 1947, Muskrat pelts: sectional and seasonal effects on grades. — Jour. Wildl. Mgt. 11: 153—161.
KERÄNEN, J., 1946, Lämpötilan normaaliarvot (1901—30). Temperaturens normalvärden (1901—30). — Kuukausikatsaus Suomen sääoloihin. Ilmatiet. Keskuslaitcs 40, 9—11. Helsinki.
KIVIRIKKO, K. E., 1940, Suomen selkärankaiset. Vertebrata Fennica. — Porvoo—Helsinki.
KLEMOLA, V. M., 1936, Metsästys ja riistatalous. (Suomen Maantieteen käsikirja pp. 587—598.) — Helsinki.

— 1937a, Finnish Game and hunting. — Silva Fennica 40: 1—27.
— 1937b, Piisamimyyrästä ja siitä saaduista kokemuksista. — Laatokan Kalastajaseurojen Liitto ry. Vuosikirja 1936: 1—12.
KORHONEN, V. V., 1952, Keskimääräinen sademäärä vv. 1885—1935 (mm). Nederbördens normalvärden 1886—1935 (mm). — Kuukausikatsaus Suomen sääoloihin. Ilmatiet. Keskuslaitos 45, 5—6.
KORVENKONTIO, V. A., 1923, Huomiota piisameille. — Metsälehti 1923: 7.
— 1924, Kronobyn piisamimyyrät. — Metsästys ja Kalastus 13, 174—180, 211—214.
— 1925, Piisamimyyrä. — Helsinki.
— 1926, Niitä näitä Hämeen piisamimyyristä. — Metsästys ja Kalastus 15: 423—431.
— 1929a, Piisamimyyrästä. — Suomen Turkiskasvattajain Liiton Vuosikirja 1929: 89—95.
— 1929b, Turkiskauppa maailmankaupassa. — Turkistalous 1.
— 1930, Piisamimyyrä ja vesikasvit. — Suomen Turkiseläinten Kasvattajien Liiton Vuosikirja 1930: 19—45.
KOSKELO, E., 1931, Piisameista. — Turkistalous 3: 115—116.
— 1932, Piisameista. — Ibid. 4: 97—98.
KOSKI, Y., 1946, Älä riko luonnon järjestystä. — Metsästys ja Kalastus 35: 174—177, 206—208.
KOTILAINEN, M. J., 1956, Vorläufiges über die Wasserchemie der Stratiotes-Seen in Kittilä, Finnisch-Lappland. — Arch. Soc. 'Vanamo' 10, 2: 153—160.
KRUMMES, W. T., 1940, The muskrat a factor in waterfowl habitat management. — Trans. N.Am. Wildl. Conf. 5: 395—398.
KÄHKÖNEN, J., 1946, Ketut ja piisamimyyrät. — Metsästys ja Kalastus 35: 191.
KÖPPEN, W., 1931, Grundriss der Klimakunde. — Berlin und Leipzig.
LAMPIO, T., 1946, Riistataudit Suomessa vv. 1924—43. (Summary: Game diseases in Finnland 1924—43.) — Suomen Riista 1: 93—142.
— 1949, Piirteitä ketun ravinnosta. — Metsästys ja Kalastus 38: 129—131.
— 1950, Ketun vahingollisuus eri maiden ravintotutkimusten valossa. — Erämies 5, 9: 1—3.
— 1951, On the significance of predators in the control and dispersal of the diseases of game. — Pap. Game Res. 6: 3—20.
— 1953, Tutkimuksia ketun ravinnosta. (Summary: On the food of the fox.) — Suomen Riista 8: 156—164, 229—230.
LANTZ, D. E., 1926, The muskrat as a fur bearer, with notes on its use as food. — US Dept. Agric. Farmer's Bull. 869. Washington. 20 pp.
LAVROV, N. P., 1931, Ондатра. Пушные звери СССР, N:o 7.
— 1933, Некоторые данные по питанию ондатры. (Zusammenfassung: Einige der Tatsachen über die Nahrung Bisamratte Fiber zibethicus L.) — Зоол. журнал 12: 67—79.
— 1950, Половой цикл и продовитость ондатры в бассейне среднего течения Сыр-Дарьи. — Тр. Всес. Н.-И. ин-та охотничьего промысла, 9: 36—45.
— 1953, Внутренние и наружные паразиты ондатры. — Ibid. 12: 132—155.
— 1955a, Изменения и прогноз численности ондатры. — Ibid. 14: 5—19.
— 1955b Динамика ареала и промыслового значения ондатры в СССР. — Зоол. Журнал 34: 441—453.
— 1957, Акклимитизация ондатры в СССР. — Москва
LAY, D. W., 1945, Muskrat investigations in Texas. — Jour. Wildl. Mgt. 9: 56—76.
— & TED O'NEIL, 1942, Muskrats on the Texas coast. — Jour. Wildl. Mgt. 6: 301—311.
LE COMPTE, E. L., 1925, The muskrat industry in Maryland. — Bull. Cons. Dept. Md. Game Div. Baltimore. 67 pp.
LEHTOLA, H., 1932, Suomen Lapin piisameista. — Turkistalous 4: 58.
LEONARD, W. W., & R. F. GORMAN, 1946, Beautiful new mutations in muskrats. — Fur Trade Jour. Can. 24. (According to Wragg, L. E., 1953.)
LILJA, S., 1932, Piisami rahaa tuottamaan. — Turkistalous 4: 82—83.
LILJESTRÖM, G., 1954, Bisam in Norrbotten. — Svensk Jakt 92: 341.
LIRO, J. I., 1924, Biisamimyyrä. — Luonnon Ystävä 28: 79—86.
— 1925, Biisamimyyrä (Fiber zibethicus). — Maatalouskoelaitoksen maamieskirjasia 10. Helsinki. 47 pp.
LOHAMMAR, G., 1938, Wasserchemie und höhere Vegetation schwedischer Seen. — Symb. Bot. Upsal. III; 1—252.

LUNDBERG, S., 1955, Översikt över Sveriges däggdjurs- och fågelfauna 1954. — Sveriges Natur 2A: 178—201.

LUTHER, A., 1952, Über den natürlichen Fundort von Anodonta piscinalis Liss. — Mem. Soc. F.Fl. Fenn. 27: 80—83.

LYNCH, J. I., T. O. O'NEIL and D. W. LAY 1947, Management significance of damage by geese and muskrats to gulf coast marshes. — Jour. Wildl. Mgt. 11: 50—76.

MARISTO, L., 1941, Die Seetypen Finnlands auf floristischer und vegetationsphysiognomischer Grundlage. — Ann. Bot. Soc. Zool. — Bot. Fenn. 'Vanamo' 15, 5: 1—312.

MARVIN, M. J., 1939, Акклиматизация ондатры в группе Кончезерских озер Карельской АССР. I (Summary: The acclimatization of the musk-rat in the lakes in the vicinity of the lake Kontch in the Karelian ASSR.) — Труды карельского государственного педа гогич. инст, I: 69—92.

MATHIAK, H. H., 1948, Wisconsin Fur Research, Quarterly Progress Rep. VII: 3. — Wisc. Dept. Cons. Madison. (According to Bednarik 1956).

— 1952, Principles of level ditching for muskrat management. — Wisconsin Conserv. Bull. 17: 14—16.

— & J. B. HALE, 1953, Survival and productivity studies. — Ibid. 12: 133—135.

MATTHEWS, H. L., 1952, British mammals. — London.

MCCANN, L. J., 1944, Notes on growth, sex and age ratios, and suggested management of Minnesota muskrats. — Jour. Mammal. 25: 59—63.

MCLEOD, J. A., and G. F. BONDAR, 1952, Studies on the biology of the muskrat in Manitoba. Part I. — Canad. Jour. Zool. 30: 243—253.

MCNAMARA, L. G., 1949, Salt-marsh development at Tuckahoe New Jersey. — N.Am. Wildl. Conf. 14: 100—117.

MEHL, S., 1931, Beiträge zur Anatomie und Entwicklungsgeschichte der Bisamratte. — München.

MERISALO, L., 1944, Mikä on piisamin kohtalo? — Metsästys ja Kalastus 33: 187—188.

MERRIAM, C. H., 1884, The mammals of the Adirondack Region. — New York.

MIEGEL, B., 1953, Die Biologie und Morphologie der Fortpflanzung der Bisamratte. — Z. mikrosk. anat. Forsh. 58: 531—598.

MOHR, ERNA, 1933, The muskrat, Ondatra zibethica (Linnaeus), in Europe. — Jour. Mammal. 14: 58—63.

Monthly surveys of the Meteorological Office in Finland. Kuukausikatsaus Suomen sääoloihin 1928—59. — Ilmatiet. Keskuslaitos. Helsinki.

MUHOJÄRVI, E., 1927, Kuultua ja nähtyä Tuuloksen ja Hauhon piisamimyyristä. — Suomen Kalastuslehti 34: 21—26.

MURIE, A., 1936, Following fox trails. — Univ. Michigan Mus. Zool. Misc. Publ. 32: 1—45.

MÜLLER, G., 1952, Die Herkunft der Bisamratte in Mitteleuropa. — Wiss. Zschr. Martin Luther-Univ. Halle—Wittenberg I, Mat. Naturwiss. Reihe 1/2: 129—137.

— 1953, Beiträge zur Anatomie der Bisamratte (Ondatra zibethica). — Ibid. 5: 817—865.

MÖRSKY, R., 1958, Riistan esiintyminen metsästyskauden 1957/58 päättyessä. (Summary. Game populations in Finland at the end of the 1957/58 hunting season.) — Suomen Riista 12: 175—176.

NELSON, A. L., 1933, A preliminary report on the winter food of Virginian foxes. — Jour. Mammal. 14: 40—43.

NIKITINA, N. A., 1958, Особенности использования территории полевыми мышами (Apodemus agrarius Pall.). (Summary: Peculiarities of territory utilization by the mice, Apodemus agrarius Pall.) — Зоол. журнал 37: 1397—1408.

NORRLIN, J. P., 1871, Flora Kareliae Onegensis I. — Notiser Sällsk. F. Fl. Fenn. Förhandl. 13. Ny ser. 10: 1—183.

NOVIKOV, G. A., 1936a, Акклиматизация ондатры в юго-восточной Карелии. (Zusammenfassung: Akklimatisation der Ondatra im südöstlichen Karelien.) — Труды Бородинской биологической станции 7 B, 2: 139—163.

— 1936b, Акклиматизация ондатры на Кольском полуострове. (Summary: The acclimatization of the ondatra on the Kola penin-sula.) — Вопросы экологии и биоценологии B, 3: 184—207.

ODUM, E. P., 1949, Small mammals of the highlands (North Carolina) plateau. — Journ. Mammal. 30: 179—192.
OJASTI, J., 1952, Tutkimuksia ja havaintoja piisamista. — Molekyyli 8: 8—11.
OLIN, T. V., 1936, Suomen vesistöjen alueet ja järvet. — Finlands vattenområden och deras sjöar. — Die Wassergebiete Finnlands und ihre Seen. — Hydrografisen Toimiston Tiedonantoja 7: 1—68.
O'NEIL, T., 1949, The muskrat in the Louisiana coastal marshes. — New Orleans Louisiana Dept. Wildl. and Fisheries. (According to BEDNARIK 1956.)
OSGOOD, F. L., 1938, The mammals of Vermont. — Jour. Mammal. 19: 435—441.
OSGOOD, H. H., 1900, Results of a biological reconnaissance of the Yukon River region. Annoted list of mammals. — N. Am. Fauna 19: 21—45.
— 1901, Natural history of the cook inlet region, Alaska. — N. Am. Fauna 21.
OLSEN, P. F., 1959a, Dental patters as age indicators in muskrats. — Jour. Wildl. Mgt. 23: 228—231.
— 1959b, Muskrat breeding biology at Delta Manitoba. — Ibid. 23: 40—53.
PANCOAST, J. M., 1937, Muskrat industry in southern New Jersey. — Trans. N.Am. Wildl. Conf. 2: 527—530.
PIRNIE, M. D., 1941, Muskrats in the duck marsh. — Ibid. 6: 308—312.
PORSHILD, A. E., 1945, Mammals of the McKenzie delta. — Canad. Field-Nat. 59: 4—22.
PUSTET, A., 1933, Ein Versuch zur Frage der Wanderung der Bisamratte. — Prakt. Bl. Pflanzenbau und Pflanzenschutz 1933: 61—68. (According to HOFFMANN 1958.)
— 1936, Die Bekämpfung der Bisamratte in Deutschland 1935/36. — Nachrichtenbltt. Dtsch. Pflanzenschutzdienst 16: 115—119.
RAEKALLIO, J., 1938, Kilpeenjoen musta piisami. — Suomen Kalastuslehti 35: 205—207.
RAND, A. L., 1948, Mr. W. H. Pryenton's notes on Manitoba mammals of the Herb Lake Flin Flon area. — Canad. Field-Nat. 62: 140—150.
RENQVIST, H., 1932, Kasvillisuuden peittämä osa Suomen järviä. — Terra 44, 47—56.
— 1952, Inland waters. (Suomi, a general handbook on the geography of Finland, pp. 161—201.) — Helsinki.
ROBERTS, H. A., and R. C. EARLY 1952, Mammal survey of southeastern Pennsylvania. — Final Rep. Pittman-Robertson Proj. 43-R. Pennsylvania Game Comm. Harrisburg, Pa. 70 pp.
ROEST, A. J., 1951, Mammals of the Oregon caves area, Josephine county. — Jour. Mammal. 32, 345—351.
ROSLUND, H. R., 1951, Mammal survey of Northcentral Pennsylvania. — Final Rep. Pittman-Robertson Proj. 37-R. Pennsylvania Game Comm., Harrisburg Pa. 55 pp.
RUSTAD, O. A., 1952, Carnivorous behavior in the muskrat. — Jour. Mammal. 33: 114.
RÄSÄNEN, V., 1930a, Havaintoja Kurkijoelle istutetuista piisameista. — Turkistalous 2, 133—134.
— 1930b, Lisätietoja Kurkijoelle istutetuista piisameista. Ibid. 2: 150.
SALONEN, J., 1956, Über das Vorkommen der Hydrophyten in den Stratiotes-Seen in Kittilä, Finnisch Lappland. — Arch. Soc. 'Vanamo' 10, 2: 146—152.
SARAVUORI, V., 1933, Tietoja piisamimyyrän (Fiber zibethicus) esiintymisestä ja levinneisyydestä Etelä-Hämeessä. — Unpublished M. A. thesis. University of Helsinki.
SATHER, 1954, The dentition method of aging muskrats. — Chicago Acad. Sci., Nat. Hist. Misc. 130: 1—3.
— 1958, Biology of the Great Plains muskrat in Nebrasca. — Jour. Wildl. Mgt., Wildl. Monographs 2: 1—35.
SCHILDER, F. A., 1956, Lehrbuch der allgemeinen Zoogeographie. — Jena.
SCOTT, T. G., 1943, Some food coactions of the northern plans red fox. — Ecol. Monogr. 13: 427—479.
SEEMANS, R., 1941, Muskrats in the Champlain Valley of Vermont, Lake Champlain Fur Survey. — Vermont Fish & Game Service, State Bull. 3—4: 1—34.
SELIN, INGER, 1956, Riistaeläinten esiintyminen metsästyskauden 1955/56 päättyessä. (Summary: Game populations in Finland at the end of the 1955/56 hunting season.) — Suomen Riista 10: 198—199.
— 1957, Riistaeläinten esiintyminen metsästyskauden 1956/57 päättyessä. (Summary: Game populations in Finland at the end of the 1956/57 hunting season.) — Ibid. 11: 159—160.

SEMENOV, B. T., 1950, Акклиматизация ондатры в Архангельской области и Коми АССР. — Тр. Всес. н.-и. ин-та охотничьего промысла, B. IX: 3—20.
SHANKS, C. E., and G. C. ARTHUR 1952. Muskrat movements and population dynamics in Missouri farm ponds and streams. — Jour. Wildl. Mgt. 15: 138—148.
SHIRAS, G., 1921, The wild life of Lake Superior, past and present. — National Geogr. Mag. 40, 2: 113—204.
SIIVONEN, L., 1951, Suomen Riistanhoito-Säätiön riistatiedustelujen pätevyydestä. (Summary: On the reliability of the game inquiries of the Finnish Game Foundation.) — Suomen Riista 6: 149—154, 192—193.
— 1956, Suuri nisäkäskirja (Mammalia Fennica). — Helsinki.
— 1957, Peltopyy- ja rusakkokantojen vaihteluista ja niiden perussyistä sekä katojen torjumisesta. (Summary: On fluctuations in partridge and field hare populations and on their basic causes, as well as on the prevention of population lows.) — Suomen Riista 11: 7—28.
— & AIRI VÄÄNÄNEN, 1951, Riistan esiintyminen metsästyskauden 1950/51 päättyessä: (Summary: Game populations in Finland after the 1950/51 hunting season.) — Ibid. 6. 166—169, 195—196.
SIRÉN, A., 1955, Suomen vesistöalueet ja keskimääräiset valuma-arvot. (Ref.: Die Gebietflächen und mittleren Abflusspenden der Flüsse Finnlands.) — Hydrografisen toimiston tiedonantoja 15: 1—127.
SMITH, F. R., 1938, Muskrat investigations in Dorchester County, Maryland, 1930—34. — U.S. Dept. Agric. Circ. 474: 1—24. 24 pp.
SOOTER, C., 1946, Muskrats of Tule Lake Refuge, California. — Jour. Wildl. Mgt. 10: 68—70.
STEARNS, L. A., and M. W. GOODWIN, 1941, Notes on the winter feeding of the muskrat in Delaware. — Jour. Wildl. Mgt. 5: 1—12.
— D. MACCREARY, and F. C. DAIGH 1939, Water and plant requirements of the muskrat on a Delaware tidewater marsh. — Proc. 26th Ann. Meet. N. J. Mosquito Extermination Assoc.
— 1940, Effect of ditching for mosquito control on the muskrat population of a Delaware tidewater marsh. — Univ. Delaware Agric. St. Bull. 225, Technical 26. 55 pp.
STEVENS, W. E., 1953, The northwestern muskrat of the MacKenzie Delta Northwest Territories, 1947—48. — Canad. Wildl. Serv. Wildl. Mgt. Bull. 1, 8: 1—40.
STORER, T. I., 1938, The muskrat as native and as alien. — Calif. Fish and Game 24: 159—175.
SUOMALAINEN, E. W., 1923, Harkitsematon toimenpide. — Metsästys ja Kalastus 12: 115—117.
SVIHLA, A., & R. D. SVIHLA, 1931, The Louisiana muskrat. — Jour. Mammal. 12: 12—28.
SÖYRINKI, N., 1939, Ein Beitrag zur Kenntnis der Verbreitung der höheren Wasserpflanzen in der alpinen Stufe Fennoskandiens. — Ann. Bot. Soc. Zool. — Bot. Fenn. 'Vanamo' 11, 3: 35—40.
TAKOS, M. J., 1947, A semi-quantitative study of muskrat food habits. — Jour. Wildl. Mgt. 11: 331—339.
TIITOLA, E., 1938, Piisamirantojen hoidosta. — Pellervo 36: 85—87.
TRETPAK, P., 1955, Лиеа и ондатра. — Природа 8.
TRIPPENSEE, R. E., 1948, Wildlife management I. Upland game and general principles. — New York.
— 1953 Wildlife management II. Fur bearers, waterfowl and fish. — New York, Toronto, London.
TURČEK, F. J., 1957, Zur Verbreitung der Bisamratte, Ondatra zibethica (Linné, 1766), in der Slowakei. — Säugetierkundl. Mitt. 5: 101—106.
TURUNEN, A. J., 1948, Ketun kolttosia piisamin pesillä. — Metsästys ja Kalastus 37: 350.
ULBRICH, J., 1930, Die Bisamratte, Lebensweise, Gang ihrer Ausbreitung in Europa, wirtschaftliche Bedeutung und Bekämpfung. — Dresden.
ULVINEN, A., 1937, Untersuchungen über die Strand- und Wasserflora des Schärenhofes am mittleren Mündungsarm des Flusses Kymijoki in Südfinnland. — Ann. Bot. Zool. — Bot. Fenn. 'Vanamo' 8, 5: 1—252.
VAARAMA, A., 1938, Wasservegetationsstudien am Grossee Kallavesi. — Ann. Bot. Soc. Zool. — Bot. Fenn. 'Vanamo' 13, 1: 1—314.
VALLI, J., 1931, Piisamimyyrä vahinkoa tuottavana kalanviljelyksillä. — Suomen Kalastuslehti 38: 204.

VALTONEN, T., 1959, Piisami kalmojuuren levittäjänä. — Lounais-Hämeen Luonto 6: 30—34.
VASILJEV, E. A., 1939, Паразитофауна ондатры. (Summary: The parasitic fauna of the musk-rat). — Тр. Карельского гос. пед. ин-та, I. B: 93—100.
VELTHUYSEN, H., 1954, Bisamråttan. — Svensk Jakt 92: 128—130, 146.
VINOGRADOV, B. S., & I. M. GROMOV, 1952, Грызуны фауны СССР. — Определитель по фауны СССР. Москва 48: 264—265.
VITÉ, J. P., 1950, Ökotop. Ein Beitrag zur Definition des Umweltbegriffes. — Oikos 2: 271—274.
VOIPIO, P., 1946, Kuolevatko hilleri ja vesikko sukupuuttoon maassamme. — Metsästys ja Kalastus 35: 40—43.
— 1948, Riistan laadun parantaminen ja sen biologiset edellytykset. (Summary: Improving the quality of the game and the biological requirements therefore.) — Suomen Riista 2: 7—76.
— 1950, Evolution at the population level with special reference to game animal and practical game management. — Pap. Game Res. 5: 1—176.
VÄÄNÄNEN, AIRI, 1952, Riistan esiintyminen metsästyskauden 1951/52 päättyessä. (Summary: Game populations in Finland after the 1951/52 hunting season.) — Suomen Riista 7: 171—172, 188.
— 1953, Riistan esiintyminen metsästyskauden 1952/53 päättyessä. (Summary: Game populations in Finland at the end of the 1952/53 hunting season.) — Ibid. 8: 190—191, 204.
— 1954, Riistan esiintyminen metsästyskauden 1953/54 päättyessä. (Summary: Game populations in Finland at the end of the 1953/54 hunting season.) — Ibid. 9: 191—192.
WARD, R. Dec., and C. F. BROOKS, 1938, The climates of North America. Mexico, United States, Alaska. (KÖPPEN, W. und R. GEIGER, Handbuch der Klimatologie II, J: 1.) — Berlin.
WARWICK, T., 1934, The distribution of the muskrat (Fiber zibethicus) in the British Isles. — Jour. Animal Ecol. 3: 250—267.
— 1940, A contribution to the ecology of the musk-rat (Ondatra zibethica) in British Isles. — Proc. Zool. Soc. London 110A: 165—201.
WERESTSCHAGIN, N. K., 1939, К вопросу об экологических нишах и морфологических адоптациях. (Resumè. Sur les niches ecologiques et adaptations morphologiques.) — Bull. Soc. Nat. Moscou, S. Biologique 48, 1: 43—52.
WIJNGAARDEN, A. van, 1954, Biologie en bestrijdning van de woelrat Arvicola terrestris terrestris (L.) in Nederland. — Plantenziektenkundige Dienst te Wageningen, Mededeling 123: 1—147.
WILSON, K. A., 1955, Litter production of coastal North Carolina muskrats. — Proc. SE Assn. Game & Fish Comms., New Orleans La. Nov. 1, 2: 13—19.
WRAGG, L. E., 1953, Notes on the life history of the muskrat in southern Ontario. — Canad. Field-Nat. 67: 174—177.
YEAGER, L. E., 1943, Fur production and management of Illinois drainage system. — Trans. N.Am. Wildl. Conf. 8: 294—301.
Yearbooks of the Hydrographic Bureau. Vuosikirja-Årsbok 10—15, Hydrografinen Toimisto 1932—1955. — Helsinki 1936—57.